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# The Median Lingual Process of Frogs: A Bizarre Character of Old World Ranoids Discovered in South American Dendrobatids

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## ABSTRACT

Unexpected discovery of a median protuberance on the tongue of several *Colostethus* spp.(Dendrobatidae) provides first knowledge of an unusual anatomical structure in New World frogs. The general term *median lingual process* is suggested for all similarly positioned structures, previously known only in certain Asian and African frogs of the superfamily Ranoidea. References to the process are mostly buried in taxonomic descriptions under the term "median papilla," although it is many times larger than the tongue's fungiform papillae (which carry taste receptors) and the still smaller filiform papillae. Scanning electron microscopy shows a cell-surface ultrastructure of microridges (and microknobs) as is characteristic of certain other epithelia. The function of the median process is unknown but conceivably involved in the sophisticated anuran chemosensory system.

From a survey of museum specimens and literature, the median process is shown to occur in one or more species of at least 16 genera of three nominal families and several subfamilies of Old World ranoids. Considerable variation in the median lingual process was found and is *preliminarily* classified under several morphologies. **Type A:** Retractile, upright cone-shaped processes occur with α-type retraction in *Discodeles*, *Indirana*, *Mantidactylus*, *Rhacophorus*, and with β-type retraction in *Platymantis* and possibly *Staurois*. **Type B:** Retractile, upright rugose processes with α-type retraction characterize *Petropedetes* only. **Type C:** Elongate, longitudinally reclining processes characterize several genera of the Petropedetinae—*Arthroleptides* with α-type retraction, *Dimorphognathus*, *Ericabatrachus*, and *Phrynodon*, retraction unknown, *Nothophryne*, possibly nonretractile, and *Phrynobatrachus*, apparently both retractile and nonretractile. **Type D:** Retractile and nonretractile bumps or other exceptionally short structures occur in various arthroleptines, petropedetines, and ranines—probably a reflection of parallel reduction in both type-A and type-C processes.

Overall homology of the several types of lingual process is tenuous and suggested only by the widespread existence of a retractile mechanism in the Old World ranoids and the apparent loss of such a mechanism in some but not all African petropedetines and in South American *Colostethus*. In dendrobatid *Colostethus*, the median lingual process is seemingly nonretractile and, except for a reduced (type D) process in one species, conforms generally to the common petropedetine type (type C), resembling most closely the tapered, pointed process of the East African *Nothophryne*.

The median lingual process therefore looks to be homologous at least in the Dendrobatidae and African Petropedetinae. However, scanning electron micrographs show differences in dorsal tongue-surface morphology that have yet to be put in systematic context: *Colostethus* has a lingual covering of filiform papillae (as in *Rana* etc.), whereas at least some petropedetines have the mucosal epithelium folded and ridgelike (as in *Bufo* and *Bombina*). But *Colostethus* and petropedetines similarly have a collar of cilia encircling the taste disc (as in *Rana* etc. but lacking in *Bufo* and *Bombina*).

Although current molecular evidence (Ruvinsky and Maxson, 1996) places the Dendrobatidae within South American Bufonoidea (= Hyloidea), the lingual process suggests that dendrobatids are

New World ranoids, as originally indicated by Cope and Boulenger and more recently by Ford (1993). Still remaining to be investigated is the possibility (Noble, 1922–1931; Lynch, 1971) that dendrobatids may in some way be related to Neotropical Elosiinae (= Hylodinae), whose relationships are not clear. In arguing against Noble's hypothesis and promoting a dendrobatid-ranid relationship, Griffiths (1959) misinterpreted dendrobatid thigh musculature and other characters, whereas Noble's anatomical observations have been corroborated.

*Colostethus atopoglossus*, new species, is among the dendrobatids having a median lingual process. It is a small, web-footed frog from cloud forest of the Cordillera Occidental, western Colombia. It is similar to *C. lacrimosus* Myers in having a lingual process, paired cloacal tubercles, and a distinct, white postocular stripe running obliquely from eye to arm. *Colostethus atopoglossus* is larger and is bright yellow-orange on the posterior belly and underside of thighs, whereas the smaller *C. lacrimosus* is ventrally white with grayish thighs. Both are riparian, but *C. atopoglossus* is an active, extremely abundant montane forest frog at elevations of 1800 to 2260 m, whereas *C. lacrimosus* is found in Pacific-side lowland rain forest (< 700 m), where it is secretive and believed to exist in low population densities.

## RESUMEN

El hallazgo inesperado de una protuberancia medial en la lengua de varias *Colostethus* spp. (Dendrobatidae) representa el primer conocimiento de una estructura anatómica extraordinaria en ranas del Nuevo Mundo. Se sugiere el término general *proceso lingual medial* para todas las estructuras de posición similar, conocidas anteriormente sólo en algunas ranas asiáticas y africanas de la superfamilia Ranoidea. Las referencias al proceso en su mayoría están escondidas en descripciones taxonómicas bajo el término "papila medial [median papilla]," aunque es muchas veces mayor que las papilas fungiformes de la lengua (que llevan los receptores gustatorios) y las papilas filiformes, que son más pequeñas aun. Microscopía electrónica de barrido revela una ultraestructura de microcrestas ["microridges"] y microbotones ["microknobs"] sobre la superficie celular, lo cual es característico de algunos otros epitelios. La función del proceso medial es desconocida pero posiblemente está involucrada en el sofisticado sistema quimiosensorial de los anuros.

Una revisión de especímenes de museo y la literatura reveló que el proceso medial se presenta en una o más especies de por lo menos 16 géneros de tres familias y subfamilias nominales de los Ranoidea del Viejo Mundo. Se observó un grado de variación considerable en el proceso lingual medial, lo cual se clasifica preliminarmente bajo varias morfologías. **Tipo A:** Procesos retráctiles, verticales de forma conica, ocurren con retracción de tipo-α en *Discodeles*, *Indirana*, *Mantidactylis*, *Rhacophorus* y con retracción de tipo-β en *Platymantis* y posiblemente *Staurois*. **Tipo B:** Procesos retráctiles, verticales, rugosos con retracción de tipo-α, caracterizan a *Petropedetes* únicamente. **Tipo C:** Procesos alargados, longitudinalmente reclinados, caracterizan a varios géneros de Petropedetinae—*Arthroleptides* con retracción de tipo-α, *Dimorphagnathus, Ericabatrachus* y *Phrynodon* con tipo de retracción desconocido, *Nothophryne*, que es posiblemente no-retráctil y *Phrynobatrachus*, que es aparentemente tanto retráctil como no-retráctil. **Tipo D:** Estructuras muy bajas, poco protuberantes, retráctiles o no, ocurren en varios arthroléptinos, petropedétinos y ráninos—probablemente un reflejo de una reducción paralela en los procesos de tipos A y C.

La homología general de los distintos tipos de procesos es tenue, sugerida únicamente por la distribución amplia de un mecanismo de retracción en los Ranoidea del Viejo Mundo y la aparente pérdida de tal mecanismo en algunos, mas no todos, de los petropedétinos africanos y en los *Colostethus* suramericanos. En el género dendrobátido *Colostethus*, el proceso lingual medial es aparentemente no-retráctil y (excluyendo un proceso reducido de tipo-D) conforma generalmente con el tipo común de los petropedétinos (tipo-C), con una mayor similitud con el proceso ahusado, puntiagudo de *Nothophryne* de Africa Oriental.

Parece entonces que el proceso lingual medial es homólogo por lo menos entre los Dendrobatidae y los Petropedetinae africanos. Empero, micrografías de microscopía electrónica de barrido muestran diferencias en la morfología de la superficie dorsal de la lengua que aun no se han analizado en un contexto sistemático: *Colostethus* tiene una cubierta lingual de papilas filiformes (al igual que *Rana* etc.), mientras que al menos algunos petropedétinos presentan el epitelio mucoso doblado en una forma parecida a cordilleras (como lo tienen *Bufo* y *Bombina*). Pero tanto los *Colostethus* como los petropedétinos comparten un collar de cilias que circundan al disco gustativo (lo mismo que en *Rana* etc. pero ausente en *Bufo* y *Bombina*).

Aunque la evidencia molecular actual ubica a Dendrobatidae entre los Bufonoidea (= Hyloidea) suramericanos (Ruvinsky y Maxson, 1996), el proceso lingual sugiere que los dendrobátidos son ranoideos del Nuevo Mundo, como lo indicaron originalmente Cope y Boulenger y más recientemente Ford (1993). Aun queda por investigarse la posibilidad (Noble, 1922–1931; Lynch, 1971) de que los dendrobátidos estén de alguna manera relacionados con los Elosiinae (= Hylodinae) del Neotrópico, cuyas relaciones no están claras. En su argumento contra la hipótesis de Noble para promover una relación entre los dendrobátidos y los ránidos, Griffiths (1959) interpretó mal la musculatura del muslo y otros caracteres en dendrobátidos; por el contrario, las observaciones anatómicas de Noble han sido corroboradas.

Entre los dendrobátidos que presentan un proceso lingual medial se incluye *Colostethus atopoglossus*, una nueva especie palmeada de bosque nublado de la Cordillera Occidental del oeste de Colombia. Es muy parecida a *C. lacrimosus* Myers, con la cual comparte el proceso lingual, un par de tubérculos cloacales y una franja distintiva postocular que pasa oblicuamente entre el ojo y el brazo. *Colostethus atopoglossus* es más grande y presenta un color amarillo-naranja en la parte posterior del abdomen y la superficie ventral de los muslos, mientras que la más pequeña *C. lacrimosus* es ventralmente blanca con muslos grisáceos. Ambas son ribereñas, pero *C. atopoglossus* es una rana activa y extremadamente abundante que habita en el bosque montañoso entre 1800 y 2260 m de altura, mientras que *C. lacrimosus* se encuentra en bosques de tierra baja (< 700 m) del Pacífico, donde es secretiva y se cree que existe en densidades poblacionales muy bajas.

## INTRODUCTION

*Ex Dendrobatidae semper aliquid novi!*

The main purposes of this paper are to report the occurrence of a median lingual process in certain New World frogs of the family Dendrobatidae and to begin inquiry into its phylogenetic significance. Inasmuch as this very peculiar structure has been individually reported for a variety of Asian and African ranoid frogs, we were puzzled to find that it has not attracted wider attention and that few zoologists seem aware of its existence. For that reason, we have attempted a brief comparative study of the gross morphology, variation, and taxonomic distribution of the median lingual process in Old and New World taxa. We also speculate on its possible function and describe the new species of *Colostethus* that initially drew our attention to the structure.

The amphibian tongue has been consistently mentioned in taxonomic descriptions for a very long time (e.g., Duméril and Bibron, 1841: 131). But the only extensive, comparative review of the tongue in amphibians is that of Magimel-Pelonnier (1924), who did not include dendrobatids in his work or any of the ranoids that were known to possess a lingual process. Nor is the structure mentioned by more recent workers who examined the anuran tongue in search of evolutionary significance (Griffiths, 1963: 243; Regal and Gans, 1976; Horton, 1982). Among general texts, we found a brief reference to the lingual process only in Noble (1931: 523).

Although the lingual process is ignored in the general literature and often overlooked in taxonomic accounts, it nonetheless is mentioned in many original and secondary descriptions of Asian and African ranoids—a few examples being Boulenger (1882), Bourret (1942), Dubois ("1986" [1987]), Dutta and Manamendra-Arachchi (1996), Inger (1954), Poynton (1964), Taylor (1921), and Witte (1934).

Usually, the process is mentioned simply in the context of a present-or-absent character useful in distinguishing taxa. It is most often called a median "papilla"—but papillae are expected on tongues and the term seems to have camouflaged a novel structure from further attention. Owing to the potential for confusion with the tongue's other, much smaller papillae, we prefer to call it the *median lingual process*.

This also prevents potential confusion with the ubiquitous "lingual premetamorphic papillae" of anuran larvae—presumed taste organs that occur on the tongue anlage (Hammerman, 1967, 1969; Helff and Mellicker, 1941; Wassersug, 1976, 1980; Wassersug and Heyer, 1988). Helff and Mellicker (1941: 350) noted that the premetamorphic papillae

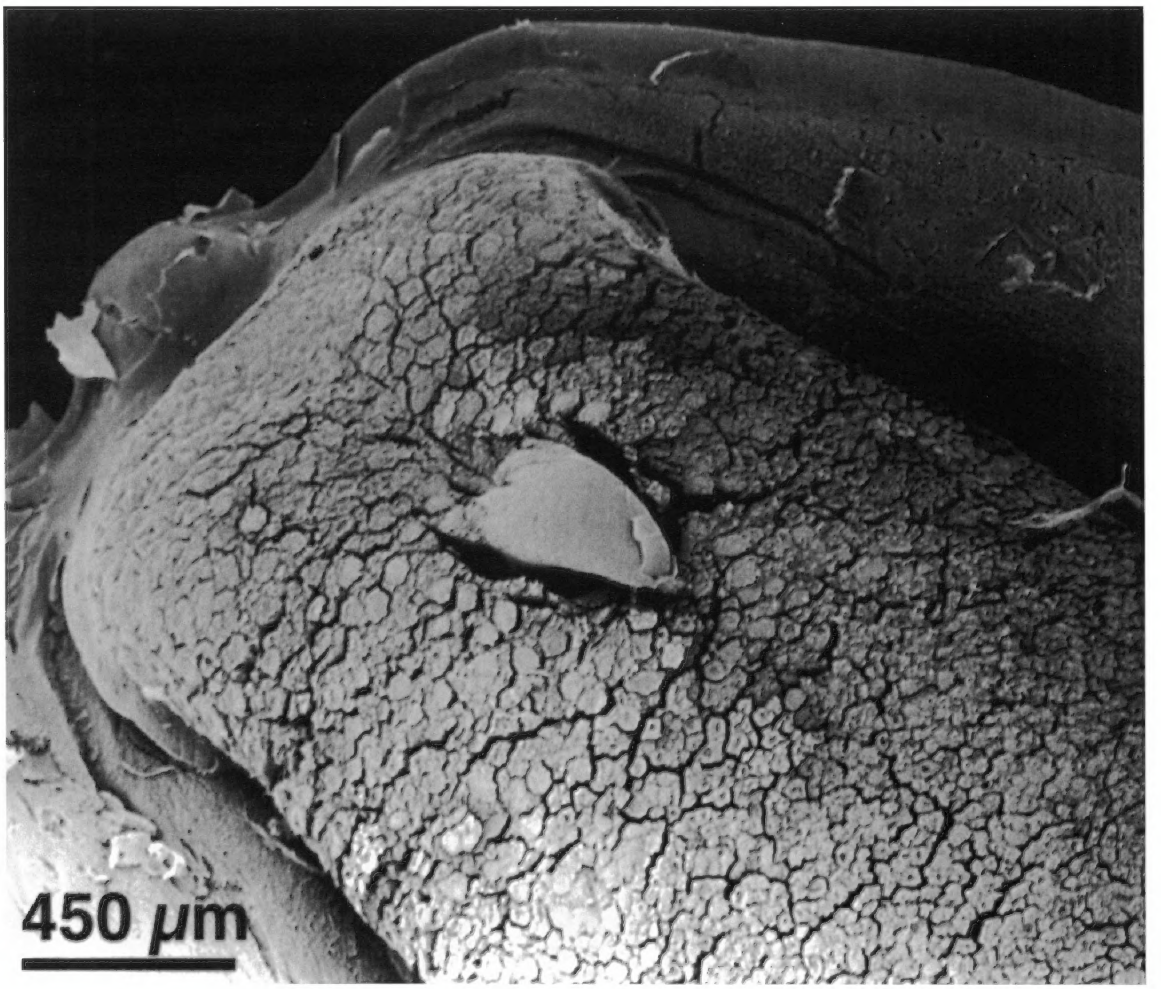


Fig. 1. Scanning electron micrograph of the dorsal surface of the tongue of *Colostethus atopoglossus*, new species, UVC 10134, showing the position and orientation of the median lingual process. The anterior end of the lower jaw points to the upper left, with the lingual process pointed posteriorly toward the free end of the tongue.

develop before the tongue anlage and that they "seem to be little more than evaginations of the mouth floor, since their epithelium and corium resemble very closely those of the floor." These papillae, which disappear with tongue development, are usually paired or multiple structures arranged about the midline and therefore seem unlikely to be homologous with the single, median lingual process discussed here. Nonetheless, the histogenesis of the median lingual process remains to be studied, as does the underlying anatomy of the tongue (our dissections to this point have been very limited). The present overview shows that the median lingual process comprises an unexpectedly variable set of structures of questionable homology.

## THE MEDIAN LINGUAL PROCESS IN DENDROBATIDAE

The lingual process was found in eight species of *Colostethus* (appendix 1) from opposite sides of northern South America: In the Venezuelan Guayana it occurs in *C. parkerae*, *C. shrevei*, and several undescribed species (Myers and Donnelly, in press). Along the western Andes of Colombia and Ecuador it is present in *C. lacrimosus* and in at least two undescribed species, including *C. atopoglossus* that is named herein.

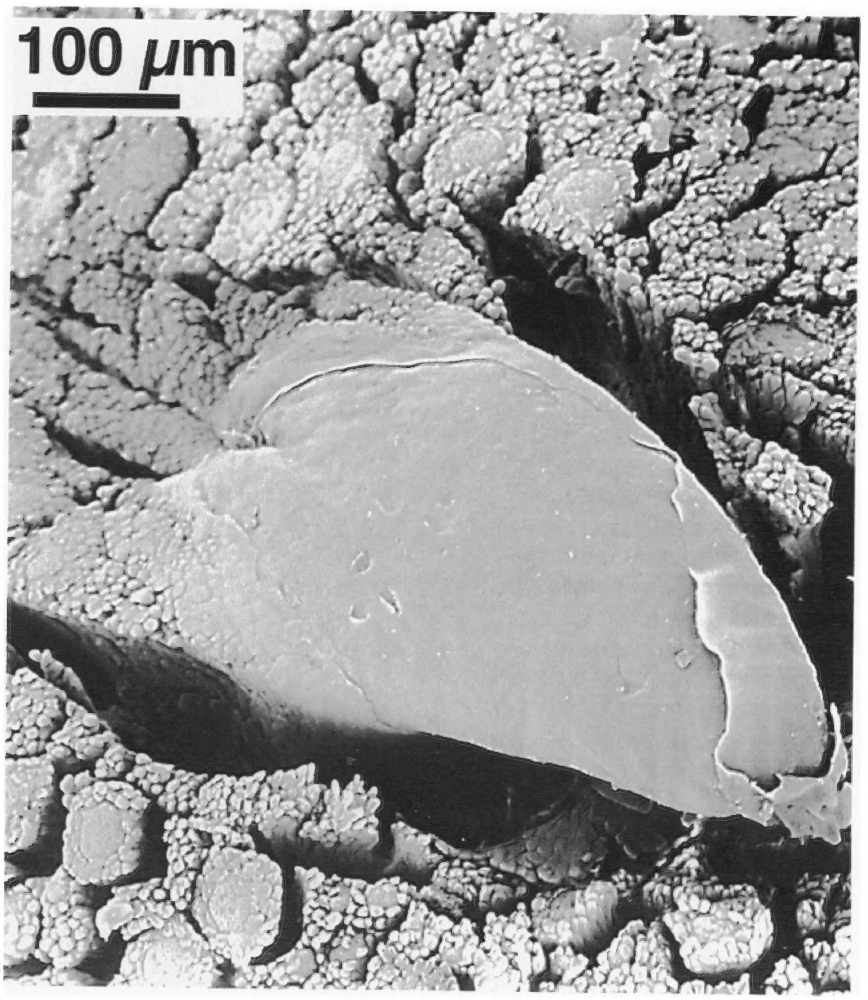


Fig. 2. Scanning electron micrograph of the median lingual process of *Colostethus atopoglossus*, from figure 1. Note the smooth surface of the lingual process except for filiform papillae at the proximal corners; the slough may be dried mucus. Visible to either side of the median process are flat-topped fungiform papillae, which carry the taste organs and which are closely surrounded by filiform papillae. Although anteriorly confluent with the dorsum linguale, the median process rises from and reclines in a deep pit, which becomes shallow and papillate posteriorly under the tip of the process.

The lingual process of *C. atopoglossus* (figs. 1, 2) is a tapering, pointed structure that extends superficially from the dorsal surface of the tongue, positioned medially and approximately one-fourth the length of the tongue from the anterior (attached) edge. The process points toward the free end of the tongue, posteriorly when the tongue is at rest. In preserved material it is either slightly raised or lies in a lingual pit roughly the same size and shape as the process; when at rest in this pit, the structure is approximately flush with the surface of the tongue and is seen under the dissecting microscope as a V-shaped cut pointed posteriorly.

Interspecific variation in the size and shape of the lingual process in *Colostethus* is quite extensive, although its position and the absence of papillae are constant. It ranges from a small, round bump in *Colostethus shrevei* (fig. 3A), to a slender, bluntly pointed process in another tepui species (fig. 3B), and to long, slender, pointed structures in others (e.g., fig. 17D in Myers and Donnelly, in press). The elongate processes are sometimes raised to an inclined position in preserved

frogs but we have seen no indication of retractility. The tip of the lingual process may extend beyond the elongate pit, the posterior part of which seems little more than a depression on the tongue's surface (as can be visualized in fig. 2); slight variations in the posterior extent of the pit possibly reflect preservation. No unambiguously discernible pit is associated with the bumplike lingual process in *C. shrevei*, in which the lingual process rises up through the papillate lingual surface.

No intraspecific variation in the expression of this character has been observed. The lingual process is present in both male and female frogs of all sizes. Several tiny juveniles (the smallest being 9.2 mm SVL) are included in the type series of *C. atopoglossus*, and all exhibit a well-developed lingual process like that in older specimens.

## THE PROCESS IN RANOIDEA AND COMPARISONS WITH DENDROBATIDS

TAXONOMIC DISTRIBUTION: The discovery of a lingual process in *Colostethus* led to a broader search in other frogs. To date, superficially similar and dissimilar lingual processes have been found only in some genera in the superfamily Ranoidea,[4] including the following 16, which are listed according to the familial and subfamilial arrangement in Frost (1985).

ARTHROLEPTIDAE: ARTHROLEPTINAE
*Arthroleptis*
RANIDAE: PETROPEDETINAE[5]
*Arthroleptides*
*Dimorphognathus*
*Ericabatrachus*
*Nothophryne*
*Petropedetes*
*Phrynobatrachus*
*Phrynodon*
RANIDAE: MANTELLINAE
*Mantidactylus*
RANIDAE: RANINAE
*Discodeles*
*Indirana*
*Micrixalus*
*Platymantis*
*Staurois*
RHACOPHORIDAE: PHILAUTINAE
*Philautus*
RHACOPHORIDAE: RHACOPHORINAE
*Rhacophorus*

Voucher specimens are listed in appendix 2. The presence of a median lingual process was confirmed in some 50 species representing 12 genera; for some of these genera, additional species could be added from the literature, which in some cases would lead into a nomenclatural morass best avoided at this point.

We have used the literature, however, in order to add several additional genera to the above list. The monotypic petropedetine genera *Ericabatrachus* (Largen, 1991) and *Phrynodon* (Parker, 1935) are included based on the original descriptions. The ranine genus *Micrixalus* and the rhacophorid genus *Philautus* are included based on various sources. A few other genera (*Schoutedenella* and *Ingerana*) are excluded for reasons discussed under Sources of Ambiguity.

Spot checking failed to reveal the character in other genera of the above subfamilies or in the arthroleptid subfamily Astylosterninae or in the ranoid families Hemisotidae, Hyperoliidae, or Microhylidae (a large group sometimes placed in its own superfamily). We cannot state that it is absent in these groups, only that it was not seen in specimens of representative species. The literature is vast and we undoubtedly have overlooked pertinent leads that would have been useful for this brief survey.

### GENERAL POINTS OF SIMILARITY

Although the size and shape of the median lingual process within Old World Ranoidea varies considerably (figs. 3–7), there are several features in common with New World *Colostethus*.

1. The median lingual process is situated medially and anteriorly atop the tongue—dorsal to some part of the underlying insertion of the tongue musculature (never on the posterior free part of the tongue).

2. The median lingual process usually appears smooth under the dissecting micro-

[4] For content, see the two classifications presented by Dubois ("1986" [1987]: 34; 1992: 309). Monophyly of the Ranoidea is accepted as a working hypothesis, although evidence for this needs elaborating (see Ford and Cannatella, 1993: 110).

[5] = Phrynobatrachinae, auctorum (see Frost: 1985: 439).

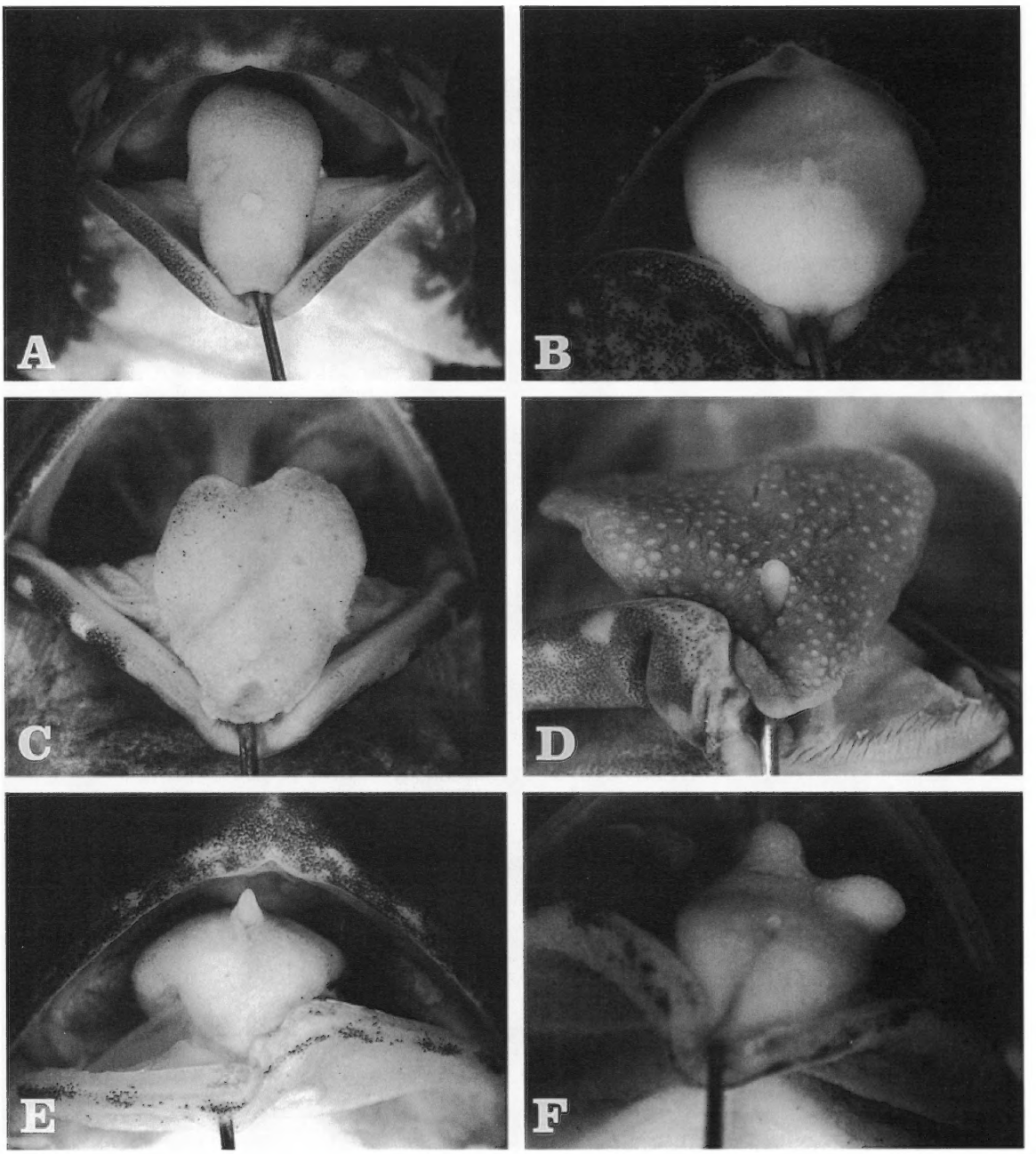


Fig. 3. The median lingual process in some dendrobatid (A, B), arthroleptine (C, D), and rhacophorine (E, F) frogs. **A.** *Colostethus shrevei* (MCZ 28567♀, holotype 22 mm SVL), Venezuela, ×7.6. **B.** *Colostethus* sp. (AMNH [CWM 19337♀, 25 mm SVL]), Auyantepui, Venezuela, ×8.4. **C.** *Arthroleptis stenodactylus* (AMNH 56104♀, 20 mm SVL), Nyasaland (Malawi), ×10.2. **D.** *Arthroleptis variabilis* (AMNH 9020♀, 35 mm SVL), Belgian Congo (Zaire), ×10.0. **E, F.** *Rhacophorus macropus* (AMNH 74211♂, 28 mm SVL; 74210♂, 30 mm SVL), Sri Lanka, protruded (E, ×7.6) and partially retracted processes (F, ×7.3).

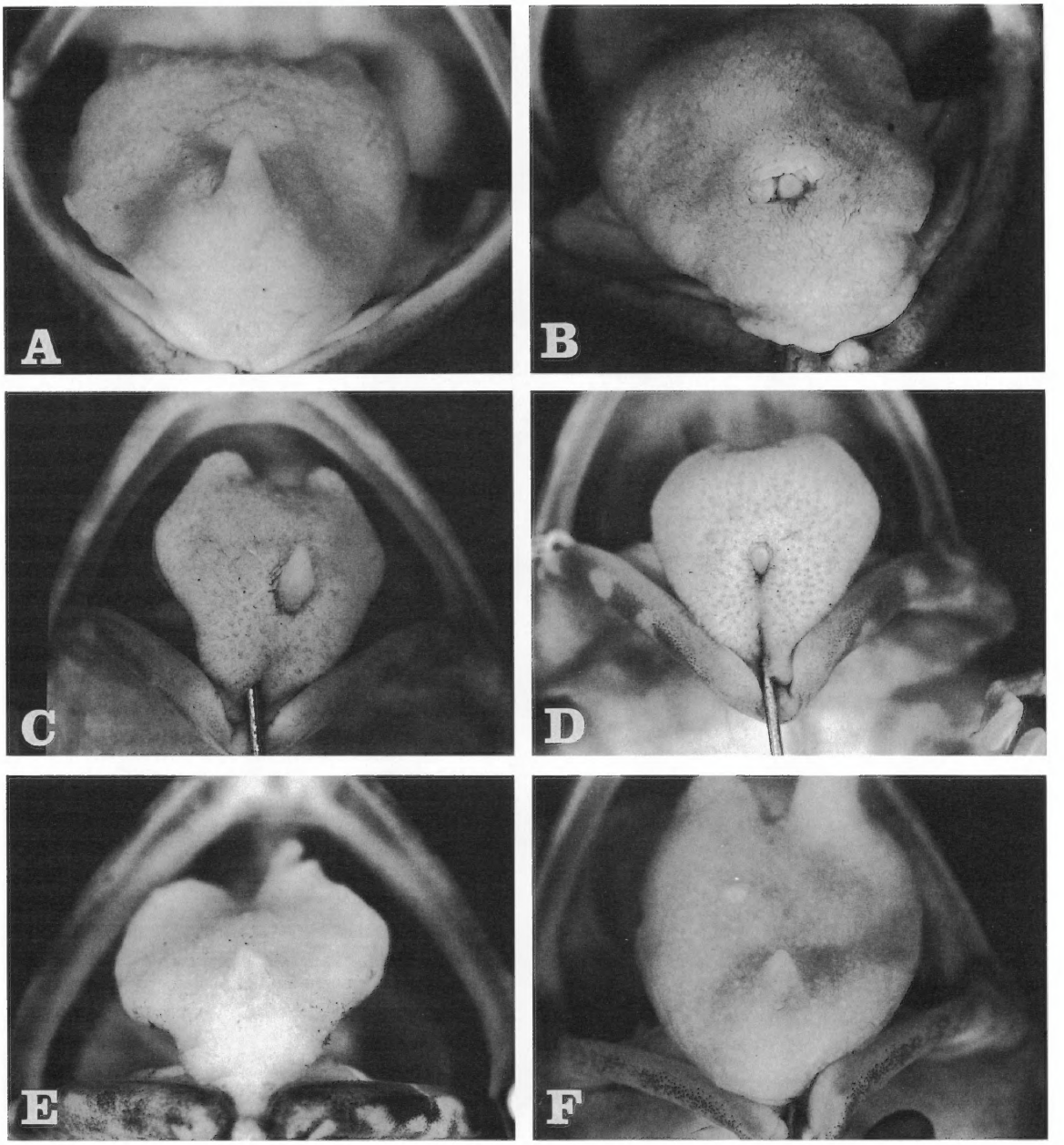


Fig. 4. The median lingual process in some mantelline (A, B) and ranine (C–F) frogs. **A, B.** *Mantidactylus femoralis* (AMNH 50367♀, 40 mm SVL; 50366♂, 38 mm SVL), Madagascar, protruded (A, ×7.6) and retracted processes (B, ×5.5). **C, D.** *Indirana leithii* (AMNH 40034♀, 24 mm SVL; 63509♂, 25 mm SVL), India, protruded (C, ×8.0) and retracted processes (D, ×7.2). **E.** *Platymantis dorsalis* (AMNH 88045♀, 36 mm SVL), Philippines, ×7.0. **F.** *Staurois natator* (AMNH 70013♂, 31 mm SVL), Philippines, ×7.7.

scope and lower magnifications of the scanning electron microscope (see Surface Ultrastructure for high magnification). In *Colostethus atopoglossus*, for example, the lingual process is free of papillae except proximally, where there are filiform papillae on each side of the dorsal base (fig. 2). Examination under the light microscope also shows the lingual process to be smooth in most Old World ranoids examined, the main exceptions being

*Petropedetes* (fig. 6F), in which the rugose process is textured similar to the surrounding lingual surface, and *Platymantis*, in which the surface is minutely folded and ridged (fig. 5B). Sparse fungiform papillae were seen on the low, poorly developed lingual process of *Discodeles guppyi*; such papillae, which carry the gustatory organs or taste buds, may well have gone unnoticed in other species characterized by retractile cone-shaped processes (see below).

3. The median lingual process is movable and probably under voluntary control, although there seem to be taxonomic differences in the mechanisms and extent of movement, as implied below.

4. There is little or no variation in presence or absence of the median process within species. It is present in all specimens of *Colostethus* spp. that possess the structure, including juveniles. The possibility of sexual or ontogenetic variation was not rigorously examined in the Old World ranoids, but such variation was not detected in the occasional species sample that included males, females, and juveniles. See comments under Sources of Ambiguity (The Lingual Process Concealed).

### Retractile versus Nonretractile

When dealing with spirit-preserved frogs, the fact that the median process can in some species be retracted into the tongue becomes unambiguously evident only after examining a number of conspecific specimens in which the protuberance has, for some reason, become fixed in different positions. The musculature involved in retraction and protraction of the lingual process remains to be studied, but, superficially, there seem to be at least two types of retraction:

**Type α Retraction:** The most common type of retractility is best visualized by comparing photographs of the protruded and retracted processes in single species (e.g., figs. 3E, F, 4A, B, and 4C, D). Type α retraction seems to co-occur with progressive invagination of tissue around the base of the median lingual process, which concurrently sinks into the tongue, to rest at the bottom of a pit.

In these illustrations, the top of the median process in the retracted state is more or less level with the lingual surface. The process remains quite evident as it sits vertically in its pit.

But a short process in some cases can be retracted out of sight, leaving a variably distinct pit on the tongue's surface; this occurs, for example, in *Discodeles*, which has long been recognized as having a "retractile papilla" (Boulenger, 1920: 109). *Discodeles guppyi* has a very low process that may invert completely, with the apex forming the bottom of the pit (judged from dissection of AMNH 64276); this process would appear to be too low to be maintained in an upright position. But *Discodeles opisthodon* seems to invert normally, with the apex of the process resting above the bottom of the pit, albeit below the surface of the tongue (dissection of AMNH 35356).

Based on few specimens, type α seems to be the method of retraction in *Discodeles*, *Indirana*, *Mantidactylus*, *Rhacophorus*, *Arthroleptides*, and *Petropedetes*. Method of retraction was not determined for *Staurois*.

**Type β Retraction:** Inger (1954: 357), one of the few authors aware of retractility in the median process, noted for a species of *Platymantis* that in addition to being distinct, it also may be "retracted and indistinct." It was first suspected that this reflects a relatively short process that can be retracted more completely than in species with longer processes. But examination of *Platymantis boulengeri* reveals a different configuration of retraction than described above.

Three American Museum specimens of this New Britain endemic show different stages of retraction. One specimen (64627) has a conical process similar to the one in figure 4E. In the second specimen (64254), a pit seems to be forming anterior to and on each side of the process, which no longer retains its conical shape. In the third specimen (70074), the pit seems fully formed all around the front part of the process, which juts forward into the pit as a vertical, columnar fold of tissue. The β type retracted lingual process has lost its original shape and it does not stand free in its pit. This process has the surface minutely folded and ridged, as discernible under the light microscope.

Type β retraction has so far been confirmed only in *Platymantis boulengeri*, but presumably is more widespread at least in

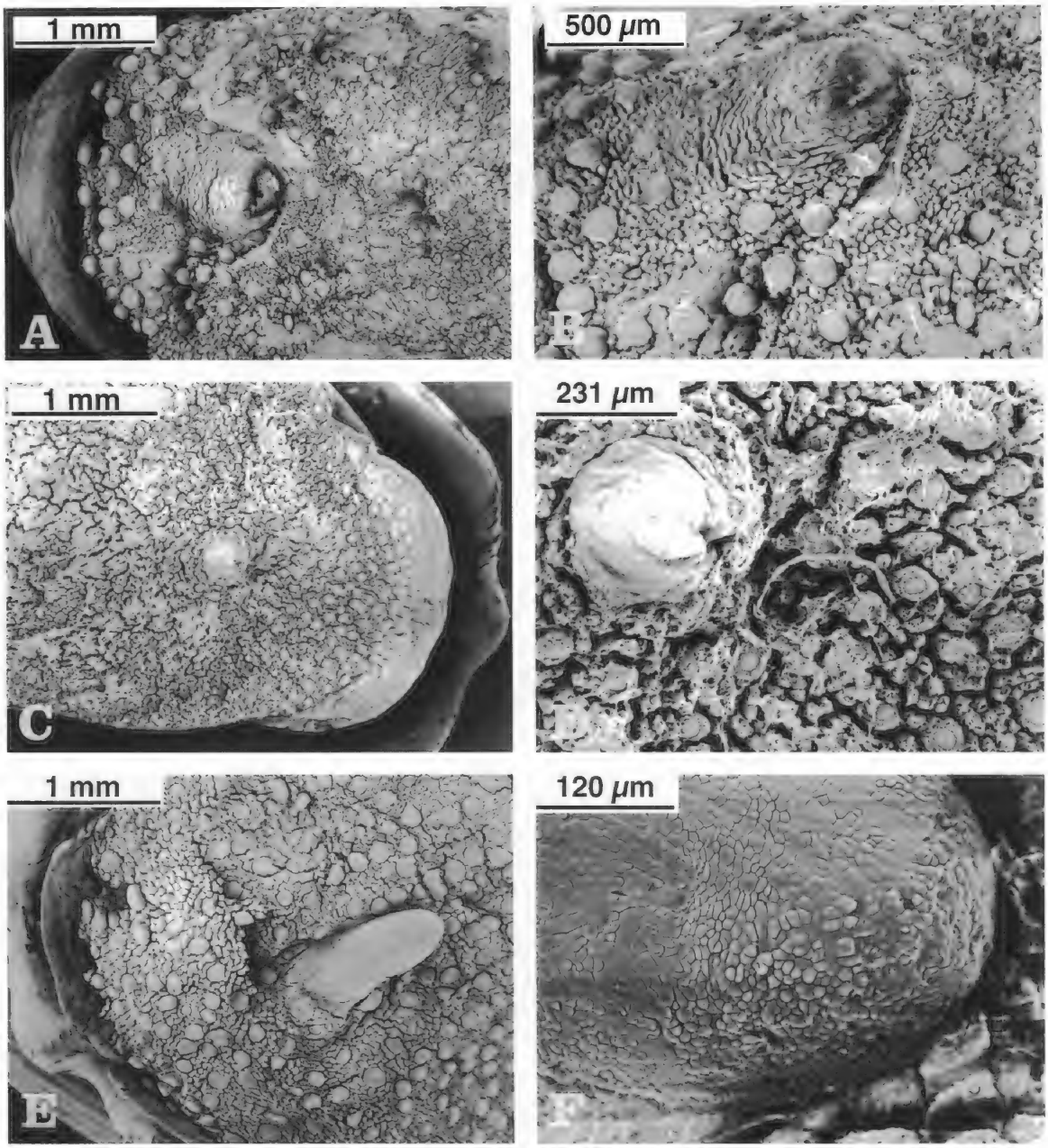


Fig. 5. Scanning electron micrographs of the tongue and median lingual process in two ranine frogs and one mantelline. **A, B.** *Platymantis dorsalis* (AMNH 88042♀, 33 mm SVL), Philippines, ×20 and ×40. **C, D.** *Discodeles guppyi* (AMNH 69310, small juv. 29 mm SVL), Solomon Islands, ×20 and ×80. **E, F.** *Mantidactylus femoralis* (AMNH 50368♀, 39 mm SVL), Madagascar, ×20 and ×85.

that genus. *Platymantis dorsalis* also has the surface of the lingual process minutely folded, which is especially evident by low power scanning electron microscopy (fig. 5A, B). This may contribute to the folding process.

It must be emphasized that presence of a median lingual pit does not automatically mean the presence of a median lingual process (see below under Pits without Processes).

Moving away from conical-shaped lingual processes described above, some frogs have elongated processes that tend to point pos-

teriorly and to recline longitudinally—into a pit of nearly conforming size in some species, with only the terminating tip being free of the pit (e.g., figs. 6A, C–E). Many of these longitudinally reclining processes seem to be nonretractile or minimally retractile—but at least the tip of the process can be raised by teasing with fine forceps or a needle, suggesting that it might be raised voluntarily by the frog. A few frogs have the lingual process represented by very short processes or even mere bumps, whose potential for movement seems varied.

These differing morphologies, associated only partly with current taxonomy, can be reduced to several basic types, as follows:

**A. Retractile, Cone-Shaped Processes with Variable Pit:** In its simplest form, the fully protruded median lingual process appears as a pointed or blunt cone of relatively smooth tissue that can sit nearly upright on the lingual surface. At this stage, a pit is either lacking (e.g., figs. 4E, F) or there is a shallow pit (e.g., figs. 3E, 4C). Concurrent with retraction as described above, a pit develops or further develops by invagination of tissue either all around the base of the median process (type α retraction) or only around its front part (type β retraction).

Retractile conical processes seem to characterize the species of Raninae examined (appendix 2), except that the very low process in *Discodeles guppyi* is listed below under the type-D processes. Retractile conical processes also were coded for the Mantellinae (figs. 4A, B) and Rhacophorinae (figs. 3E, F), although only a single species was confirmed from each of these groups. However, the situation in the one confirmed mantelline (*Mantidactylus femoralis*) is somewhat ambiguous: Figure 4A shows a fully extended conical lingual process (that has a shallow pit concealed on the posterior side) and the process is clearly retractile (fig. 4B). Some specimens in the same series of frogs have a posteriorly depressed process (fig. 5E) somewhat similar to some retractile type-C processes, suggesting either that *Mantidactylus* is misplaced in the present scheme or that type-A and retractile type-C processes are parts of a continuum. See also comment for *Arthroleptis variabilis* under the type-D processes.

Further comparisons, are likely to show that the concept of a single type-A class of conical processes is overly simplistic.

**B. Retractile, Rugose Processes with Variable Pit:** This is similar to the preceding type-A lingual process except that it has a broadly rounded apex (not conical) and has a folded, ridgelike texture like the adjacent lingual surface (see under Other Lingual Characters). It is a vertically raised, rounded projection. Type α retraction seems to occur with invagination of tissue all around the base of the process, which is withdrawn until the clearly-visible apex is about level with the lingual surface (fig. 6F).

This morphology was documented only in the petropedetine genus *Petropedetes*. The above description is a composite based on only six specimens of four species (appendix 2). The median lingual process is lacking in *Petropedetes natator*, which is distinguished by the presence of two large "fangs" (odontoids) on the front of the lower jaw.[6]

**C. Elongate, Longitudinally Reclining Processes in Pits:** This includes a variety of relatively elongate lingual processes that tend to recline on the tongue, with the tip of the process directed posteriorly, unlike types A and B, which are relatively broader at the base and which tend to stand nearly erect. A pit is always present under normal conditions.[7]

The elongate, reclining process appears to characterize several genera of the Petropedetinae (but see type B above for *Petropedetes*). The following discussion is organized under two probably artificial subdivisions of type C:

**C1. Retractile and Nonretractile (or Minimally Retractile), Blunt Processes:** These elongate, longitudinally reclining processes may be swollen and rounded like small sausages or dorsoventrally flattened.

[6] Among petropedetines, mandibular odontoids or pseudoteeth also occur in the monotypic genera *Dimorphognathus* and *Phrynodon*, both of which have a median lingual process.

[7] Exceptions seem usually to be the result of muscle contortion or protraction during preservation. Such contortion, for example, can push up the bottom of a pit, causing a horizontally elongate median lingual process to ride well above its normal level. The pit is not obvious in this condition (e.g., AMNH 11888, a specimen [not illustrated] of *Phrynobatrachus batesii*, whose normal condition is shown in fig. 6E).

They emerge from a conspicuous pit, which tends to be somewhat longer than wide (elongated posteriorly) so that, for much of its length, the posteriorly reclining process lies level with the surface of the tongue, with the blunt tip of the process usually terminally free of the pit but sometimes lying completely within an elongated pit.

*Arthroleptides*: A clearly retractile type-C process occurs in *Arthroleptides dutoiti*, one of the two named species of this genus (see also *A. martiensseni* under type D below). One specimen (AMNH 68672) of *A. dutoiti* has the elongate process retracted, with the apex flush with the tongue, whereas seven others have it reclining posteriorly as shown in figure 6A. The process has a slight distal taper and, although not acutely pointed, approaches the type-C2 process.

*Dimorphognathus*: The median process of the only species (*D. africanus*) is a nontapering, blunt structure (fig. 6C) similar to those of *Arthroleptides dutoiti* (retractile) and *Phrynobatrachus* (mostly nonretractile?). The potential for retractility could not be assessed, with only two specimens examined.

*Phrynobatrachus*: This is a large genus (64 species in Frost, 1985), of which 194 specimens of 29 species were examined for the present account. The process is characteristically blunt, as shown by *P. batesii* (fig. 6E), but *P. kinangopensis* has a slightly tapering process that is not quite pointed (fig. 7C). There are interspecific differences in the width and length of the process, but usually it is elongated roughly to the same or greater extent as shown in figures 6E, 7A, and 7C—the major exception being the relatively short process of *P. petropedetoides* (see under type D below).

The blunt tip of the process usually lies free of the posterior end of the pit (figs. 6E, 7D), but the process sometimes fits entirely into a long pit, as in specimens of *P. mababiensis* and *P. accraensis* (fig. 7B).

Superficially, these long processes appear simply to rise from the anterior end of the elongated pit in which they recline. However, the *Phrynobatrachus* process seems to be attached for much of its length along the ventral side, presumably with connective tissue or muscle holding it fast in its pit. In some species (e.g., *P. graueri*), at least the distal one-half to one-third of the lingual process seems free and potentially capable of movement, whereas in others (e.g., *P. mababiensis*, *P. accraensis*, fig. 7B) only the very tip is free.

Based on the above observations, which imply that some type-C lingual processes may be relatively fixed in position, it perhaps is not surprising that no evidence of retractility was noted in most species of *Phrynobatrachus*. Nonetheless, degrees of retractility were noted in a few species, especially *P. natalensis* (the type species) and *P. perpalmatus*. Specimens of both species were found in which the normally reclining process appeared to have been retracted to a vertical position, with only the tip showing from a rounded (contracted?) pit. This system calls for more detailed investigation than we can give here.

*Phrynodon*: This genus is tentatively classified as having a type-C1 process (rather than C2 following), but the only included species was not examined. Parker (1935: 402) described the lingual process of *Phrynodon sandersoni* as "a long median papilla."

**C2. Nonretractile (?), Pointed Processes:** Nonretractile, elongate, longitudinally reclining, pointed processes in pits characterize several species of South American *Colostethus* and possibly a few East African species of the monotypic petropedetine genera *Ericabatrachus* (*E. baleensis*, not seen) and *Nothophryne* (*N. broadleyi*, fig. 6D). The last two species have the median process elongated (nonconical) and pointed (relative to the blunt, rounded ends that characterize the median process in other genera), and at least *Nothophryne* has it markedly tapered as in *Colostethus*.

The notion that the median process may be nonretractile in these two petropedetines is speculative, inasmuch as only two specimens of *Nothophryne* and no *Ericabatrachus* were examined (the last has "a long, pointed median papilla" according to Largen, 1991: 141). The speculation is based on (1) the resemblance in general shape to the nonretractile process in *Colostethus*, and (2) the seeming nonretractility in many *Phrynobatrachus* having the C1 process, which is very similar to C2 except for the nontapering blunt ends.

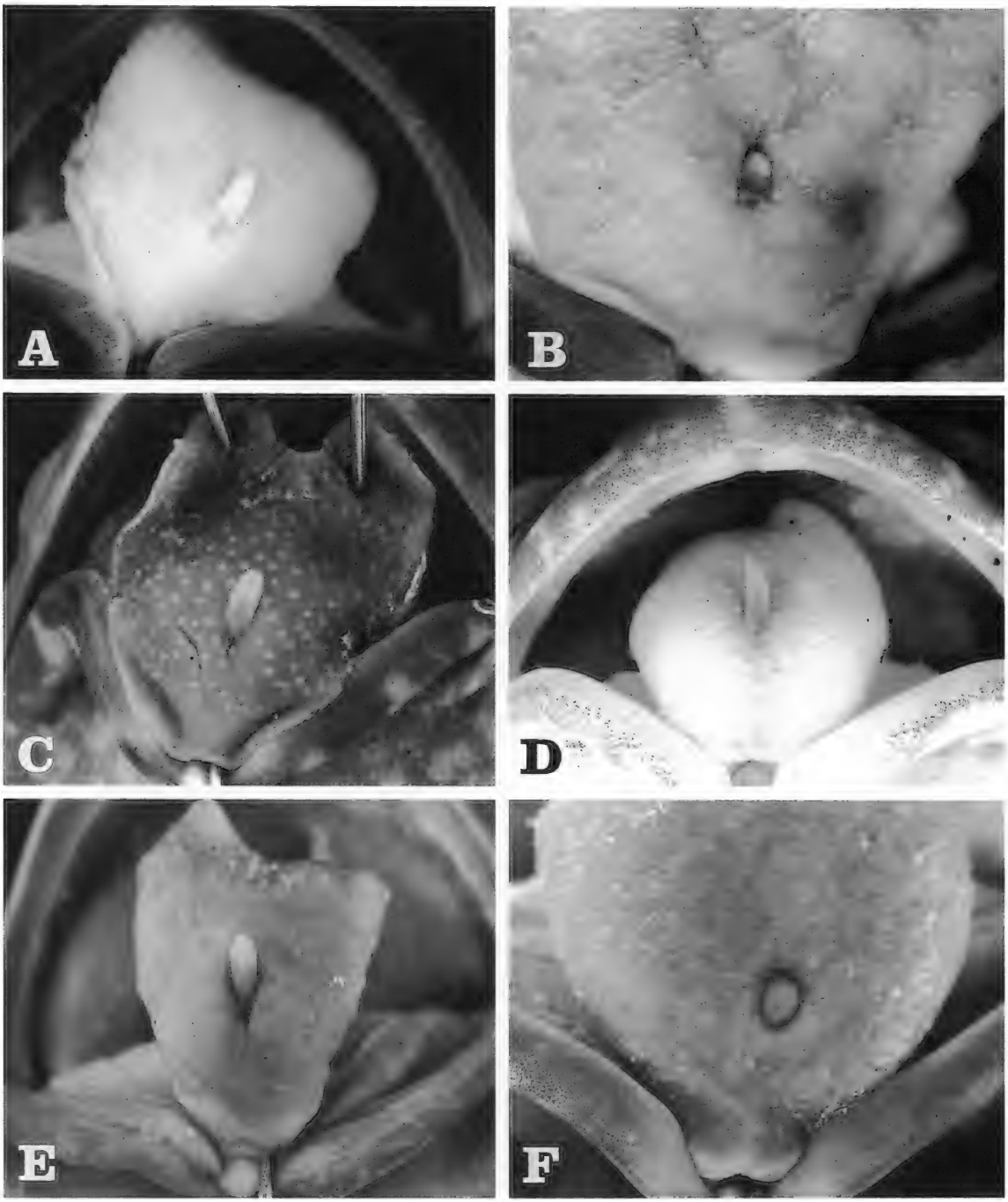


Fig. 6. The median lingual process in some petropedetine frogs. **A.** *Arthroleptides dutoiti* (AMNH 68670♀, 30 mm SVL), Kenya, ×9.7. **B.** *Arthroleptides martiensseni* (AMNH 37281♂, 59 mm SVL), Tanzania, ×6.2. **C.** *Dimorphognathus africanus* (AMNH 11890♀, 27 mm SVL), Cameroons, ×9.6. **D.** *Nothophryne broadleyi* (AMNH 95099♀, 22 mm SVL), Malawi, ×11.8. **E.** *Phrynobatrachus batesii* (AMNH 11887♂, 26 mm SVL), Kamerun, West Africa, ×11.0. **F.** *Petropedetes newtoni* (AMNH 6687♀, 38 mm SVL), Cameroon, ×7.2.

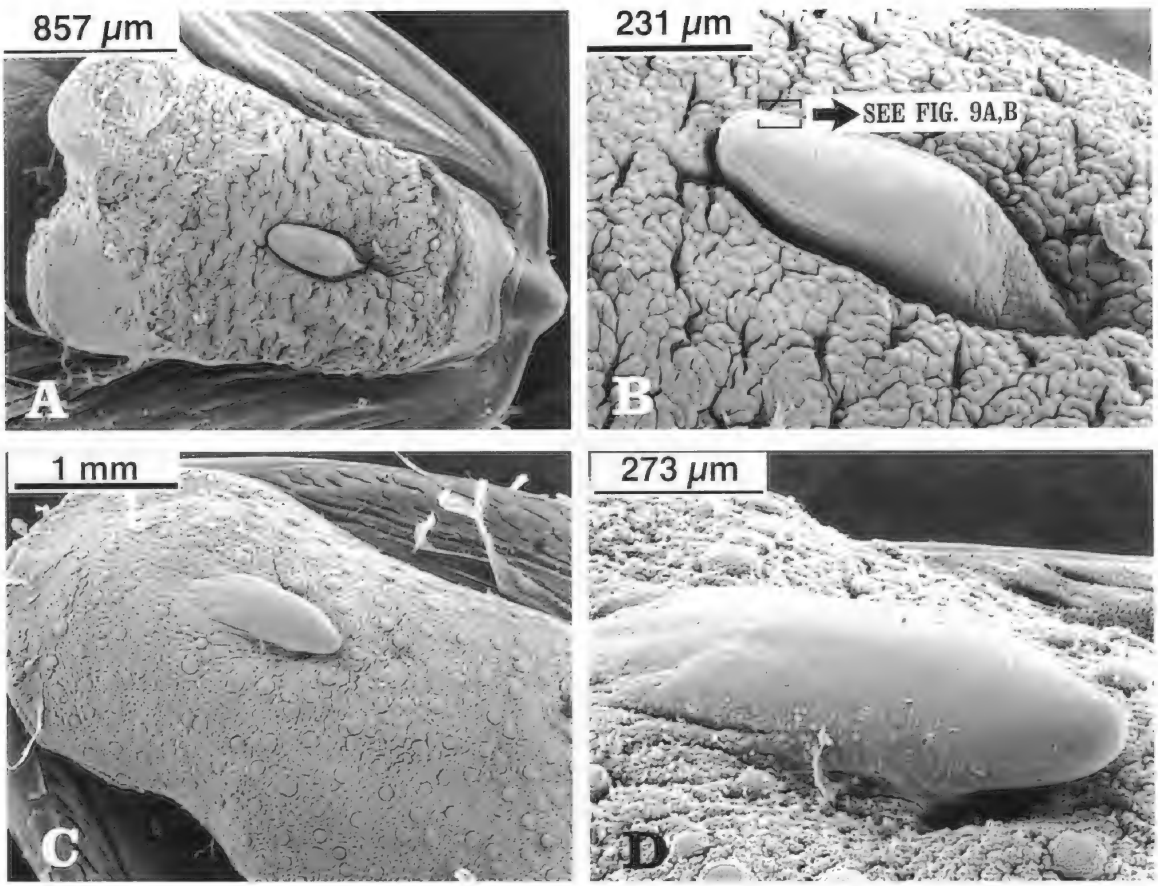


Fig. 7. Scanning electron micrographs of the tongue and median lingual process in two petropedetine frogs. **A, B.** *Phrynobatrachus accraensis* (AMNH 84623♂, 19 mm SVL), Ghana, ×25 and ×90. **C, D.** *Phrynobatrachus kinangopensis* (AMNH 87601♀, 23 mm SVL), Kenya, ×20 and ×75.

Both of these apparently nonretractile processes are ventrally adherent except for the distal (posterior) end, which is free. The median process lies entirely in a pronounced pit in this specimen of *P. accraensis*, whereas in the *P. kinangopensis* the median process is riding high, with the pit shorter than the process and only distinct posteriorly. Such differences possibly are preservation artifacts that actually reflect a continuum of dynamic change in the relative length of the median process and its associated pit.

However, individual variation in features of the tongue cannot be entirely discounted. The illustrated tongue of *Phrynobatrachus accraensis* (A) is atypical in having relatively few fungiform papillae, which are noticeably sparse in proximity to the median process (B). Other specimens of *accraensis* show a more uniform dispersion of the taste papillae.

The question of retractility aside, an elongate tapering and pointed median process seems to be present only in some *Colostethus* and in the monotypic petropedetine genus *Nothophryne* and possibly in *Ericabatrachus*. But the pointed condition is approached in a few other petropedetines (*Arthroleptides dutoiti*, fig. 6A, *Phrynobatrachus kinangopensis*, 7C), whereas the distinctly tapered process may be only bluntly pointed in *Colostethus* (fig. 3B).

**D. Nonretractile and Retractile Bumps:** This is a phenetic catchall of both retractile and nonretractile round bumps or other exceptionally short structures. They would seem to have been reduced from types A and C lingual processes. A variety of genera are represented, as follows:

*Colostethus* (Dendrobatidae): The lingual process in *Colostethus shrevei* varies from a low rounded bump to a low blunt cone that is vertically aligned and little higher than

wide (Myers and Donnelly, in press). See figure 3A.

*Arthroleptis* (Arthroleptinae): This is the only genus in the "Arthroleptidae" known to have a median lingual process (but see *Schoutedenella* under Genera Excluded). *Arthroleptis adolfifriderici*, *A. francei*, *A. poecilonotus*, and *A. stenodactylus* have very short, apically rounded to flattened processes that may be slightly inclined posteriorly in pits but which are often retracted to a vertical position. In the last position, the process may look like an undifferentiated bump that resembles the structure in *Colostethus shrevei* (compare fig. 3C with 3A). But there is no unambiguous pit or evidence of retractility in four specimens of *C. shrevei*. The lingual process is small and seems poorly differentiated in *A. tanneri*.

Of the six species of *Arthroleptis*[8] examined, the process is best developed in *Arthroleptis variabilis*, usually appearing as a short, rotund structure that is slightly reclined posteriorly (fig. 3D), but sometimes retracted in its pit in a vertical position, with only the tip visible. One specimen (AMNH 9016), of many examined, has it fully protruded in an erect position, with no evident pit, reminiscent of a type-A process; otherwise, the structure in *A. variabilis* resembles an exceptionally short type-C1 process.

*Arthroleptides* (Petropedetinae): *Arthroleptides martiensseni* has a short bumplike process that is retracted below the surface of the tongue in one specimen (fig. 6B). Its congener *A. dutoiti* has a much longer type-C1 process (fig. 6A).

*Phrynobatrachus* (Petropedetinae): Most species have a moderate to long type-C1 process, but in *Phrynobatrachus petropedetoides* it is relatively short and in some specimens it appears bumplike, probably owing to retraction.

*Discodeles* (Raninae): The low median bumplike process of *Discodeles guppyi* (figs. 5C, D) seems to be a reduced type-A process. It can apparently be concealed by complete inversion (see above under Type α Retraction).

[8] The process is lacking in the type species, *Arthroleptis wahlbergii* (AMNH 3194, 45072, 45081, 73873–73875, 99726–99732, 99995, 99996). Conclusions about the content of this genus and its familial separation from petropedetine ranids seem more based on authoritarianism than on character analysis and should be revisited.

## Sources of Ambiguity

There seems to have been no previous awareness that the lingual process or median "papilla" is as morphologically variable as demonstrated above. Consequently, most published references provide little or no information on size, shape, or orientation of the process and cannot be used to assign it even to the most common ranine (type A) or petropedetine (type C) morphotypes.

## Genera Excluded

Inadequacy of published descriptions and conflicting observations or lack of specimens were the reasons for excluding the following two genera from the list of genera and subfamilies for which the lingual process is known to be present in one or more species.

*Schoutedenella* (Arthroleptinae): In naming *Schoutedenella* and *S. globosa* (type species by monotypy), Witte (1921: 18) described a *papille conique au millieu de la langue*, mentioning in a footnote that the structure is not conspicuous (*peu distincte*) and that it was omitted from an accompanying illustration of the tongue. One of Witte's syntypes (now AMNH 68124), however, lacks a median process, and none was found in other species of *Schoutedenella* (*troglodytes*, *xenochirus*, *xenodactyloides*, *xenodactyla*) in the American Museum collection.

*Ingerana* (*Liurana*) (Raninae): The ranid subgenus *Liurana* was diagnosed partly on the recorded presence of a *papille linguale* in one species (Dubois, "1986" [1987]: 65; see also Inger, 1996: 242). The reference was to a Chinese species named *Platymantis liui* by Yang (1983), who reported a "papillate bulge" in the anterior third of the tongue. This is ambiguous because muscular protraction during preservation can, in some frogs (e.g., *Mantella*, see below), produce a prominent lingual bulge in the position where a lingual process might be expected.

## Genera Included but not Examined

The monotypic genera *Ericabatrachus* (Largen, 1991) and *Phrynodon* (Parker,

1935) are discussed above under type-C processes. The two genera below are also accepted in our list based on accounts in the literature, although the lingual processes cannot be definitely categorized from the published descriptions.

*Micrixalus* (Raninae): Dubois ("1986" [1987]: 54) stated as a diagnostic character that *Micrixalus* sometimes has a lingual process, but it seems to occur in only two of the six species that he accepted in the genus. Boulenger (1882: 94) recorded, under the name *Ixalus*, a "free, pointed papilla" in the species *opisthorhodus* (= *phyllophilus*) and *saxicola* and noted its absence in *fuscus*. Boulenger (1882: 469) appended the species *silvaticus*, for which Satyamurti (1967: 35) explicitly noted the absence of a papilla, and Pillai (1978, 1981) noted its absence in the last two species described (*nudis* and *thampii*). Boulenger (1882) usually seems to have used the phrase "conical papilla" for our type-A process, so the "free, pointed papilla" of *Micrixalus phyllophilus* and *M. saxicola* presumably is a more slender process.

*Philautus* (Rhacophoridae): The rhacophorid *Philautus* similarly contains species lacking a median process and at least one species having it, as is clear from the literature on *Philautus eximius* (Shreve, 1940, and Dutta and Manamendra-Arachchi, 1996: 162, 168). The last authors (p. 165) described the lingual process of *P. eximius* as a "conical papilla," so we guess that it is a type-A process. Some *Philautus* have a median pit (fig. 8A), which can be a source of ambiguity unless dissected (see below).

### The Lingual Process Concealed

It has been evident only to a few authors that some processes are retractable, which probably accounts for most assumptions that the process may be present or absent in the same species—or present in one taxon but not another. A few examples:

Barbour and Loveridge (1928: 209), writing about *Arthroleptis stenodactylus* (see fig. 3C), provided one of the longest statements heretofore devoted to a lingual process:

> The papilla on the tongue is absent in several half-grown frogs or is, at least, not to be detected, while it is present in other frogs from the same locality... Sometimes this papilla, as it lies in the little pit from which it springs, is flush with the level of the tongue and its prominence appears to depend not only on age but a good deal on the state of preservation of the specimen.

The median process was found in nine AMNH specimens of *A. stenodactylus*, although it originally was missed in one (AMNH 56105) in which it had retracted to the vertical position, with only a small area of tip showing. Barbour and Loveridge similarly may have overlooked the structure in some specimens. But if such a structure is sometimes hard to find with today's improved dissecting microscopes and fiber-optic lighting, workers of 70 years ago may well be excused for overlooking it. Therefore, statements that the median process is variably present within a species must be assessed cautiously. We have not encountered clearcut intraspecific variation in presence or absence in any species, although it may occur.

Presence or absence in different species is another matter, but caution is required even here. For example, Loveridge (1948: 410), under *Platymantis beauforti* (= *P. punctatus* fide Zweifel, 1969), recorded the presence of the "lingual papilla" but regarded it of dubious value in separating species, and remarked under *Platymantis boulengeri* that the tongue "had a cavity in place of papillae." His conclusion about taxonomic utility in separating species is valid only if intraspecific variation occurs or if presence of the process is hard to ascertain, which is not usually the case. His observation about a cavity in place of a papilla in *P. boulengeri* has two likely explanations: (1) The process is retracted out of sight, or (2) there is a pit only. For this species, the first explanation is correct, as already explained under Type β Retraction.

### Pits Without Processes

However, empty round pits and short longitudinal grooves do occur in species and genera that lack the lingual process, as pictured in figure 8. An obvious question: Is the presence of such cavities a vestigial clue to the evolutionary loss of a lingual process? The necessarily ambiguous answer: Possibly yes and probably no, depending on the taxon.

Inasmuch as the rhacophorid *Philautus eximius* has a conical, presumably type-A lingual process (see above), it is a reasonable hypothesis that empty lingual pits in other species are derived conditions. For example, there is no indication of a lingual process in several *P. bombayensis* (AMNH 40044–40046, 40052–40054), but a round to slightly elongate pit can be seen in all but one poorly preserved specimen. Dissection of the round pit in figure 8A reveals no indication of a retracted process.

The view of a *Mantella* tongue (fig. 8B) is more or less typical, although the groove (emphasized by underlying dark pigmentation) is not always evident. No evidence of a lingual process was found in specimens of any of the nine species of *Mantella* treated by Daly et al. (1996). Occasional specimens died with lingual muscles fixed in a protracted condition, causing a bulge on the dorsal surface. No attempt was otherwise made to survey the Mantellinae, except that a questionable type-A process was coded for a species of *Mantidactylus* (figs. 4A, B, 5E, F, and associated text). If a type-A process had been shared with a common ancestor, one might expect a rounded pit rather than a longitudinal one in *Mantella* (but see variation in *Philautus* above). As pointed out by Daly et al. (1996: 6), a convincing case has yet to be made for relating *Mantella* with *Mantidactylus*.

Poynton (1963: 326) observed that "all species of *Cacosternum* [Petropedetinae] possess a more or less distinct nick in the tongue in the position corresponding to the recess that bears the papilla in *Nothophryne*." This is not evident on all specimens but shows as a tiny slit or short groove in some (e.g., AMNH 23324, *C. boettgeri*). A similar nick or short longitudinal depression in the tongue also occurs in another petropedetine genus—the monotypic *Anhydrophryne* (e.g., AMNH 116939, *A. rattrayi*). Inasmuch as the lingual processes of other petropedetine genera often lie in elongated or longitudinal pits, homology with the condition in *Anhydrophryne* and *Cacosternum* is at least conceivable.

But anuran lingual pits and grooves always overlie some part of the tongue musculature and may reflect something else en-

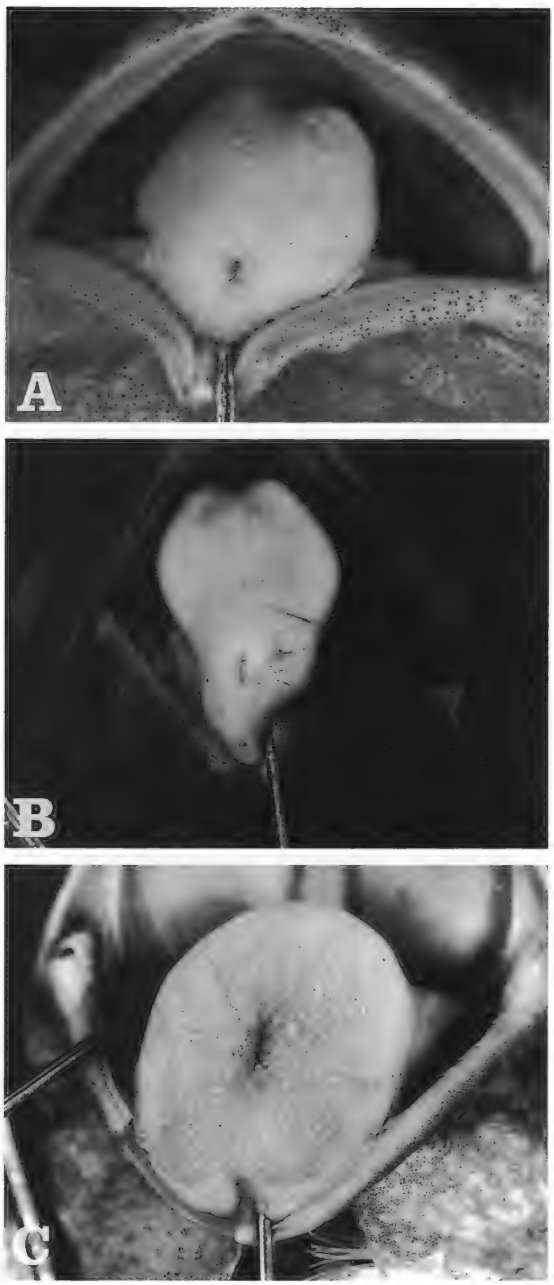


Fig. 8. Pits without processes. **A.** *Philautus bombayensis* (AMNH 40044♂, 21 mm SVL), India, ×10.0. **B.** *Mantella viridis* (AMNH 140576♂, 23 mm SVL), Madagascar, ×7.7. **C.** *Dischidodactylus duidensis*, Leptodactylidae (AMNH 23190♀, holotype 28 mm SVL), Venezuela, ×6.7.

tirely. A variable depression, sometimes forming a neat pit, occurs in the center of the tongue in one leptodactylid (fig. 8C), and diagnostic lingual grooves occur in some microhylids such as *Glyphoglossus* (Noble, 1931: fig. 174) and *Rhombophryne* (AMNH 23190).

Pits without processes have not been seen in *Colostethus* but should be watched for. Although the lingual process appears to be nonretractile in *Colostethus*, processes without clear-cut pits have not been noted except in *C. shrevei*, in which reduction of the pit is probably a derived state in parallel with reduction of the lingual process.

### Summary and Conclusions

A variably retractile, cone-shaped lingual process (type A) occurs in one or more genera of the Raninae, Rhacophoridae, and possibly the Mantellinae. One genus of the Petropedetinae is characterized by a retractile upright protuberance with a rugose surface (type B), but five other petropedetine genera have elongate processes that are either retractile or nonretractile and which lie posteriorly against the tongue in longitudinal pits (type C). Several of these groups have representatives in which the lingual process is exceptionally short, sometimes bumplike (type D). The very short processes in the Arthroleptinae seem reminiscent of both type-A and type-C processes.

The lingual process in New World *Colostethus* conforms generally to the common petropedetine type (C), but the process is tapered and the tip either acutely or bluntly pointed, as in only a few petropedetines (most have a blunt process). One *Colostethus* has a bumplike (type D) process. The spotty taxonomic distribution of the bumplike morphology suggests reduction and seems most likely to be a parallelism in dendrobatids, arthroleptines, petropedetines, and ranines.

Based on superficial structure, homology between the lingual processes in South American *Colostethus* and African petropedetine ranids is presented as a working hypothesis. It would be premature to assert that the several types of lingual processes are all homologous, although this may be indicated by their confinement to the Ranoidea (assuming monophyly of this group) and by the similar retractility of some type-A and type-C structures.

## SURFACE ULTRASTRUCTURE AND OTHER LINGUAL CHARACTERS

### Median Lingual Process

Examination of selected museum specimens by scanning electron microscopy (SEM) shows the epithelial cell surfaces of the lingual processes to be intricately patterned by raised structures. In our material, the superficial cells of lingual processes become visible at SEM magnifications approaching ×100 and their fine surface structure becomes evident at about ×1000.

The most commonly seen surface structures are **microridges** (figs. 9B, 9E), which also characterize the free cell surfaces of the fungiform papillae, or taste buds (fig. 9F), and which also have been demonstrated on the filiform papillae in *Rana* (Iwasaki et al., 1986, 1988) and on the "ridge-like papillae" in *Bufo* (Iwasaki and Kobayashi, 1988; Iwasaki et al., 1989). Microridges on frog taste receptors originally were called "microvilli" (Graziadei, 1968; Graziadei and DeHan, 1971), probably owing to poor resolution of the micrographs as well as prior use of the term in early ultrastructure studies of rabbit taste buds. Jaeger and Hillman (1976) pointed out that the structures are interconnected ridges and used the term "cytoplasmic ridges," reserving the word "microvilli" for patches of projections between the associate cells of the taste receptor and also for projections from the ridges themselves. The terms microplicae, microvillar ridges, and, especially, microridges, subsequently came into general use for such structures on a variety of epithelial surfaces, including mucoid skin epithelium (epidermis) of amphibians and fishes (Whitear, 1977: 293). Sperry and Wassersug (1976) supported earlier proposals that microridges serve a mechanical function of holding mucus to surfaces. This may be valid but may not suffice as a general explanation, inasmuch as similar microstructures occur on the dry scales of snakes and lizards (e.g., SEM micrographs in Cole and Van Devender, 1976).

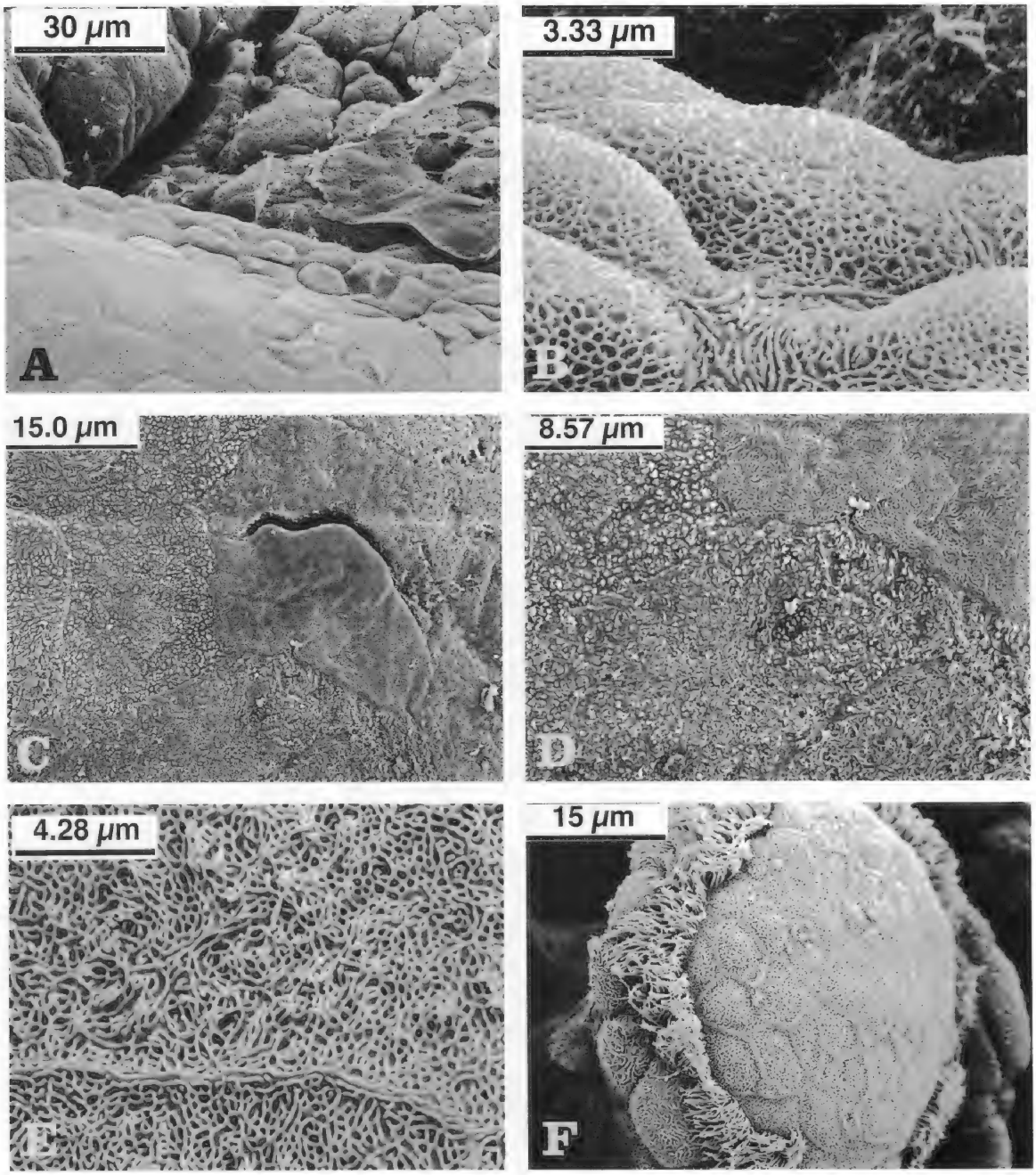


Fig. 9. Scanning electron micrographs showing ultrastructure of cell surfaces of median lingual processes and a taste receptor. **A, B.** Anterior edge of the longitudinally reclining lingual process of *Phrynobatrachus accraensis* (location shown in figure 7B), ×700 and ×6000. The calyculate or honeycomb pattern of microridges is replaced elsewhere on the process by irregularly interconnected vermiform ridges (not shown). **C, D.** Apex of small conical lingual process of *Discodeles guppyi* (figs. 5C, D), showing surface differentiation between adjacent cells, ×1300 and ×2300. Areas of vermiform microridges lie adjacent to regions of microknobs. The crevice in C may be an expansion fold. **E.** Posterior (distal) dorsal surface of the longitudinally reclining process of *Colostethus lacrimosus* (UVC 7295), ×4600. Parallel microridges demarcate cell edges across lower part of image. **F.** Fungiform papilla (taste bud) from anterior part of tongue of *Phrynobatrachus accraensis* (fig. 7A), ×1300. The papillary disc, with its clearly outlined cells, is encircled by a collar of cilia. Microridges cover the cells below the cilia as well as the surfaces of the disc cells.

There is regional variation in microridge patterning. *Phrynobatrachus accraensis*, for example, has an elegant calyculate or honeycomb pattern on the edge of the lingual process (fig. 9B) as well as dorsal areas of irregularly interconnected vermiform microridges, somewhat similar to those seen in *Colostethus lacrimosus* (fig. 9E). An additional structure, termed **microknobs** for convenience, was seen on the apex of the lingual process of *Discodeles guppyi* (fig. 9C, 9D). These are irregular little protuberances occurring adjacent to areas of microridges. The small crevice seen in figure 9C is at the very tip of the process and may be an expansion fold. The type-D bumplike lingual process of *D. guppyi* seems to be a reduced type-A process, at least some of which appear to have more flexible surfaces than type-C processes.

### Other Lingual Characters

The dorsal surface of the anuran tongue is more variable than we had anticipated, as became evident even by gross examination. Differences in pigmentation and relative conspicuousness of the fungiform papillae are evident from perusal of photographs in figures 3, 4, 6, and 8. We here note other potentially informative characters best studied by SEM. Comparative data are too sparse for systematic generalities.

The dorsum linguale is most commonly shown or portrayed as a sea of essentially nonciliated or weakly ciliated filiform papillae with a dispersion of larger fungiform papillae. The latter bear circular taste discs, seen under appropiate magnification to be surrounded by collars of cilia. Similar taste discs may be embedded in larger fields of cilia anteriorly and on the sides of the tongue, and on the palate (e.g., Düring and Andres, 1976: figs. 1, 2), but the dorsal surface of the tongue is relatively uniform and relatively free of cilia. Iwasaki et al. (1988: 62) found that ciliated cells occupied only "about 5% (by volume) of the filiform papillar epithelium" in *Rana nigromaculata*. Except for the median lingual process, the dorsum linguale of *Colostethus atopoglossus* (figs. 1, 2) fits the general pattern known in such genera as *Rana*, *Hyla*, and *Litoria* (e.g., Graziadei and DeHan, 1971: figs 2, 3; Jaeger and Hillman, 1976: figs. 1, 2; Iwasaki et al., 1986: figs. 1, 2; MacDonald, 1975).

Striking exceptions to the above pattern involve both the fungiform and filiform papillae. MacDonald (1975) briefly described the tongue in Leiopelmatidae (*Leiopelma* and *Ascaphus*) as being dorsally covered with "small ciliated papillae," with "vase-shaped 'taste-buds', 30–60 μ in diameter . . . in the apices of small papillae (Fig. 1)." The fungiform papillae in representative Bufonidae (*Bufo bufo* and *B. japonicus*) and Discoglossidae (*Bombina variegata*, *B. orientalis*) are notable in lacking the encircling collar or crown of cilia. Taste discs on the dorsum linguale in these taxa are surrounded by rounded marginal cells that appear thinner in *Bufo* than in *Bombina* (Gubo et al., 1978: fig. 15; Jasiński, 1979: figs. 2A, 4; Witt, 1993: fig. 1; Iwasaki et al. 1989: fig. 4).

Jasiński (1979) called attention to the absence of filiform papillae in *Bufo bufo*, in which the dorsal mucosal epithelium "forms high folds, dividing the surface of the tongue into numerous separate compartments." Jasiński did not comment on an earlier SEM micrograph for this species (Sagmeister et al., 1976: fig. 1) in which the individual ridge cells were labeled "filiforme Papillen."

Unaware of the reports for *Bufo bufo*, Iwasaki and Kobayashi (1988) similarly noted the absence of filiform papillae in *Bufo japonicus*, in which the dorsal tongue surface comprises "irregular undulant structures, or ridge-like papillae." Iwasaki and Kobayashi also noted the similarity of this morphology with SEM micrographs of *Bombina variegata* in Gubo et al. (1978: figs. 13–15). The situation is unclear in the telmatobiine *Calyptocephalella gayi* [= *Caudiverbera caudiverbera*], for which Stensaas (1971) mentioned both dorsal folds and filiform papillae.

A folded, ridgelike structuring imparts a different appearance to the tongue than filiform papillae do and the taxonomic distribution of the two morphologies is of interest. An undulating ridgelike surface covers the type-B lingual process as well as the tongue of *Petropedetes* (fig. 6F), which has been examined only by light microscopy. In our material, the ridgelike morphology is shown best in SEM micrographs of *Phrynobatrachus* (fig. 7). Filiform papillae are visible in

our SEM micrographs of *Colostethus*, *Discodeles*, *Mantidactylus*, and *Platymantis* (figs. 2, 5).

Although differing in presence or absence of filiform papillae, dendrobatids and petropedetines have similar fungiform papillae: a collar of cilia encircles the taste disc, at least in *Colostethus lacrimosus* (not illustrated) and *Phrynobatrachus accraensis* (fig. 9F), whereas ciliated collars are lacking in *Bufo* and *Bombina* (see above).

Therefore, among anurans having a median lingual process, there are at least two general morphologies of the surrounding tongue surface—a covering either of slender filiform papillae or a coarser folding of undulating ridges. Whether the ridgelike morphology in petropedetines is the same as in *Bufo* and *Bombina* remains to be seen. As realized by Jasiński (1979: 476), in the absence of a broader taxonomic survey, "all generalizations concerning morphology of amphibian tongue and its gustatory organs will remain impossible or highly uncertain."

## THE QUESTION OF FUNCTION

We have failed to find any reference to the functional significance of the median lingual process. We suspect that it may have something to do with feeding, but the anuran tongue serves a variety of functions, some of which can be summarily dismissed in connection with the lingual process.

Regal and Gans (1976: 722) identified four functions that correlate with the structural organization of frog tongues—namely pumping of the buccal cavity for breathing, narial closure, prey manipulation, and prey capture. The first two—respiratory pumping and narial closure—are unlikely roles. And the soft fleshy nature of the process and its size and anterior location seem to preclude it from being useful in prey manipulation. (The ability to either retract the process or to fold it into a pit may serve in part to prevent it from interfering with prey manipulation.)

The appearance and inferred voluntary control of the lingual process invite speculation that it might be used as a lure in prey capture, but there is no evidence for this. Field and laboratory observations of *Colostethus atopoglossus* failed to detect any luring or gaping and have shown only typical, visually stimulated anuran feeding behavior. As mentioned later, preliminary analyses of stomach contents of *C. atopoglossus* do not suggest any dietary specialization. Meinhardt and Parmelee (1996) similarly found that *Colostethus parkerae* is a dietary generalist.

The presence of the median process in both sexes and in juveniles (at least in *Colostethus* spp.) indicates that it does not play a role in sex recognition.

Pigmented (orange or yellow) tongues may rarely be used for intimidation in open-mouth displays (Myers, 1966), but *Colostethus* spp. have unpigmented tongues and there is no reason to think that the median lingual process might in some other way serve an antipredator function.

Chemoreception is of course a function of the anuran tongue, as is evident when frogs and toads show obvious distaste in rejecting noxious prey and also as demonstrated experimentally (Pumphrey, 1935; Sato et al., 1994a, 1994b). The lack of gustatory papillae on the lingual process of most taxa might seem to suggest that it is not an organ of taste. Nonetheless, the possibility that it serves a special sensory function—whether chemoreceptive or tactile—invites investigation.

Owing to their apparent mobility and anteromedial position, at least some lingual processes might seem well situated for a possible role in transferring substances from (or to) the anterior palate. The intermaxillary gland[9]—through various openings lying mesial and anterior to the choanae (Müller, 1932, figs. 14–20) and anterior to the vomerine teeth [when present[10]]—secretes salivary enzymes that are carried posteriorly over the palate by ciliary currents (Francis, 1961). Francis (p. 472) brought anurans into context of a "theory that the *primary* pur-

[9] The *glandula intermaxillaris* of Wiedersheim (1876), originally considered a true mucous gland, is sometimes hypothesized as being a source of mucoid adhesive that supposedly is transferred to the tongue for prey capture (e.g., Ecker, 1889: 280; Gaupp, 1904: 27; Noble, 1931: 201–202; Reeder, 1964: 102, 104). Histological evidence points to it being a "mixed" gland, with mucoserous secretions (Seifert, 1932; Francis, 1961).

[10] Vomerine teeth are lacking in some groups, including the Dendrobatidae.

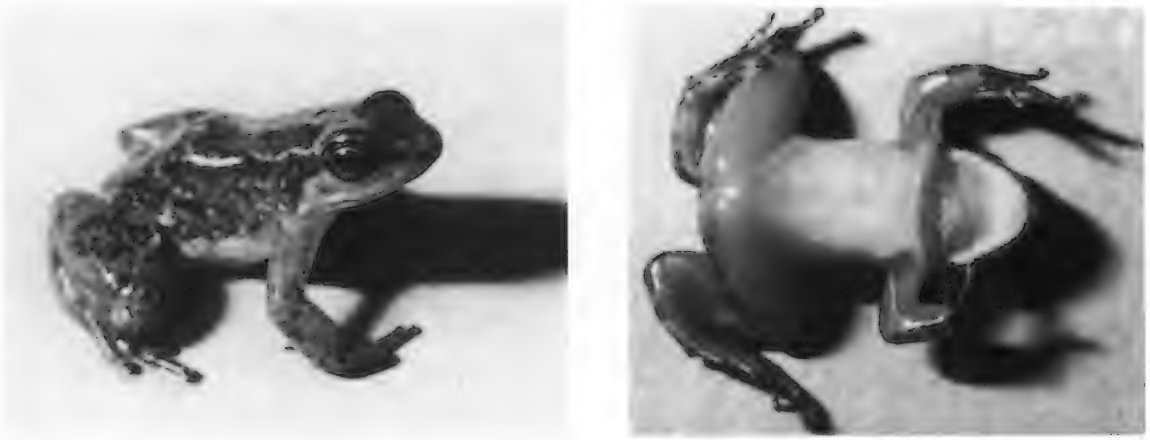

Fig. 10. *Colostethus atopoglossus*, new species, holotype UVC 12608, from color transparencies, approximately twice life size. Left: Dorsal aspect. Note the remnants of the dorsolateral stripe extending posteriorly from the corner of the eye to just behind the arm insertion. Right: Ventral aspect. Posteriorly yellow-orange; the dark color of the throat is caused by the absence of iridophores, contrasting with the white surrounding area.

pose of buccal enzymes is the liberation of substances capable of stimulating gustatory or olfactory sense receptors." He noted (p. 469) that a prey item "lacerated or punctured by the vomerine teeth will immediately liberate its tissue fluids just where they will receive the maximum concentration of intermaxillary gland secretion." Whether vomerine teeth are present or not, the ciliary currents presumably bathe the nonpapillary gustatory organs on the palate (Sato, 1976; Jaeger and Hillman, 1976).

Could compounds in the ciliary currents be further sampled and analyzed by raising the median lingual process to the anterior palate? If so, is the median process a novel chemoreceptor or only an agent of transport? In the last case, fluid transported from the palate to the tongue's dorsal surface would be brought into closer association with gustatory organs (epithelial papillary discs) atop the tongue's fungiform papillae, some of which usually lie in close proximity to the median lingual process (e.g., fig. 2).

Such lines of thought lead us to speculate that the median lingual process is an evolutionary novelty that may in some way serve the amphibian chemosensory system, which allows nonchewing predators to detect and reject noxious prey relatively rapidly. Noxiousness of insects can be caused by such agents as bitter-tasting alkaloids and formic acid, and it is not surprising that bitter and acid (as well as salt) stimuli elicit large responses from anuran taste cells and glossopharyngeal nerves, whereas sweet stimuli cause little response (e.g., figs. in Sato et al., 1994a: 767–768). Studies have not been conducted on taste cell sensitivity in any frog with a lingual process nor in the few genera of frogs that sequester at least some of their defensive skin alkaloids from arthropod prey.

We describe below the new *Colostethus* that led to the first discovery of the median lingual process in a New World frog.

### ***Colostethus atopoglossus,*** new species

Figures 1–2, 10–13

HOLOTYPE (fig. 10): Universidad del Valle, Cali (UVC) 12608 (field number TG 0695), an adult male collected calling (voucher recording TG 9606) by Taran Grant at 9:50 am on April 4, 1996, from a stick just above the water in a vegetation-covered, trickling creek running along the side of the road, El Boquerón, 2200 m, Department of Valle del Cauca, Colombia, Cordillera Occidental, 4°44′N, 76°18′W.

PARATYPES (57): UVC 10116–10134, 10141–10143, collected by M. S. Alberico and J. H. Restrepo on March 23, 1989, ca. 4 km below El Boquerón (ca. 24 km from El Cairo), ca. 1800 m, Department of Chocó.

UVC 12260–12261, collected by John D. Lynch on July 20, 1995, El Boquerón, 20.5–22.5 km from El Cairo, 2150–2200 m, Department of Chocó, Colombia. UVC 12567–12579, collected by Taran Grant on April 2, 1996, El Boquerón, 1880 m (at 4°45′41″N, 76°18′52″W) to ca. 2260 m, Department of Chocó, Colombia. UVC 12603, 12606, collected by Grant at El Boquerón, 2160–2220 m, Department of Valle del Cauca, Colombia. UVC 12611–12612, collected by Alonso Osorio on April 2, 1996, El Boquerón, 1900–2260 m, Department of Chocó, Colombia. UVC 12616–12626, collected by Fernando Castro on April 2, 1996, El Boquerón, from ca. 2000–2260 m, Department of Chocó, Colombia. UVC 12627–28, collected by Wilmar Bolívar on April 2, 1996 at 4°45′41″N, 76°18′52″W, 1880 m, El Boquerón, Department of Chocó, Colombia. UVC 12629–12631, collected by Paulo Ordóñez on April 2, 1996, El Boquerón, 1880–2260 m, Department of Chocó, Colombia.

ETYMOLOGY: The specific epithet is an adjective derived from the Greek *atopos* (odd, strange) + the compound-forming *-glossus* (-tongued).

DIAGNOSIS: A small dendrobatid similar to *Colostethus lacrimosus* with which it shares the median lingual process, essentially identical hand and foot morphology, the absence of definite body stripes in adults, similar dorsal coloration, a definite white oblique postocular stripe, the third finger not swollen in males, the black arm band absent in males, a small tympanum, a single tubercle at the base of each thigh next to the cloaca (see fig. 11),[11] and a distinct white mark on the dorsal base of the thighs on each side of the vent.

*Colostethus atopoglossus* is distinguished from *C. lacrimosus* by larger size (maximum size of males 20.7 mm SVL, females to 25.2 mm SVL in *C. atopoglossus*; *C. lacrimosus* males to 15.8 mm SVL, females to 22.1 mm SVL), ventral coloration (bright yellow groin and thighs and often ventral spotting or mottling in *C. atopoglossus*, immaculate white venter with underside of thighs pale gray in *C. lacrimosus*), and dorsal coloration of limbs in life (*C. atopoglossus* with limbs brown with yellow or orange tinge and dark brown markings, while in *C. lacrimosus* they are colored like the greenish brown dorsum). A dark head cap is present in *C. lacrimosus* and absent in *C. atopoglossus*. Population structure and elevational distribution also provide evidence for the recognition of both taxa, with *C. atopoglossus* being an extremely abundant species found from 1800–2260 m, while *C. lacrimosus* is a secretive species with low population densities known from a maximum elevation of 640 m.[12]

Both *Colostethus lacrimosus* and *C. atopoglossus* are very similar to *C. chocoensis* (Boulenger); however, *C. chocoensis* sensu stricto (i.e., not including Ecuadorian populations referred to this species) does not exhibit the lingual process.[13] *Colostethus chocoensis* further differs in lacking a definite white oblique postocular stripe and in having a well-developed fringe on the outer edge of toe 5.

MEASUREMENTS OF HOLOTYPE (in mm): All measurements were taken with dial calipers under a dissecting microscope. The holotype is an adult male (collected calling) with extremely large testes and open vocal slits. Snout-vent length 20.2; forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow 4.5; hand length from proximal edge of palmar tubercle to tip of third finger 5.7; tibia length from outer edge of flexed knee and heel 9.5; foot length from proximal edge of outer metatarsal tubercle to

[11] The cloacal tubercles were not mentioned in the description of *C. lacrimosus* but are barely visible in the photograph of paratype AMNH 110789 (Myers, 1991: 11, fig. 6, specimen on right). The cloacal tubercles vary in degree of prominence in *C. atopoglossus* (although they are always present) and cannot be detected in all of the examined *C. lacrimosus* material; we suspect that the apparent absence may be a postmortem artifact, i.e., the tubercles may weaken over time in preservative or be lost if the epidermis is sloughed.

[12] This new elevational record for *Colostethus lacrimosus* is based on UVC 7293–7296, from Río Cajambre, Departamento del Valle del Cauca, Colombia.

[13] Examination of the holotype BMNH 1947.2.14.27, UVC 6270 (both from Colombia) and KU 172790 (from Panama) reveals that *Colostethus chocoensis* lacks a lingual process. The Ecuadorian AMNH material tentatively referred to *C. chocoensis* by Myers (1991) and at least part of that (KU 166157, 166158, 221616) referred to that taxon by Coloma (1995) have a lingual process. This affirms Myers' (1991: 1, abstract) suggestion that the Ecuadorian material "conceivably represents a different species" and provides a reliable character for its diagnosis. The Ecuadorian species will be named later.

Fig. 11. The cloacal tubercles of *Colostethus atopoglossus*, new species, UVC 12616.

tip of fourth toe 9.4; head width between angles of jaws 7.1; head length diagonally from angle of jaws to tip of snout 6.6; eye length from posterior to anterior corner 2.8; eye to nares from anterior corner of eye to center of naris 1.7; distance between centers of nares 2.9; snout length measured from anterior corner of eye to tip of snout 3.3; interorbital distance 2.6; approximate diameter of tympanum 0.9 (concealed posterodorsally).

## Description

A composite description is given for the 58 specimens included in the type series. Nineteen specimens, including the holotype, are adult males, as determined by examination of testes and presence of open vocal slits; 16 specimens are adult females, confirmed by the presence of ova and enlarged, convoluted oviducts. The remaining 23 specimens are juveniles and subadults of varying sizes. Measurements and proportions are given only for adults.

Morphology: Males 18.5–20.7 mm SVL ($\bar{x}$ = 19.7, $N$ = 19) females 21.7–25.2 mm SVL ($\bar{x}$ = 23.3, $N$ = 16). The skin is smooth, with the only two dorsal tubercles found one on each side of the cloaca on the base of the thighs (cloacal tubercles; fig. 11) ranging from protuberant to slightly flattened. There is a conspicuous white spicule just behind the angle of the jaws.

The head width between the angles of jaws is 30–37 percent of SVL and is 1.1–1.2 times greater than the head length. The snout is sloped, bluntly pointed in dorsal aspect and in profile, protruding over the jaws in profile. The loreal region is flat and vertical, not sloping outward. The canthus rostralis is well defined and sharply rounded. The eye-naris distance is 52–69 percent of eye length and 50–59 percent of snout length. The nares are slightly protuberant laterally, directed posterodorsally, visible anteriorly and barely visible dorsally. The white oblique postocular stripe is bordered posterodorsally by a supratympanic fold. The diameter of the tympanum is approximately ⅓ of the eye length; the tympanum is concealed posterodorsally. Maxillary and premaxillary teeth are present. An elongate, tapering median lingual process (type C2) is present (figs. 1, 2).

The hand is moderate in length, 22–30 percent of SVL, and 1.2–1.4 times longer than the forearm. Relative lengths of appressed fingers 3 > 4 > 2 > 1. The fingers are strongly fringed, and in some specimens the lateral fringes converge to form a basal web between fingers 2 and 3, although it is possible that this is an artifact caused by the flattening of the hand during fixing. Tuberculation consists of a round palmar tubercle, an elongate thenar tubercle at the base of finger 1, a single subarticular tubercle on fingers 1 and 2, and two on fingers 3 and 4. The finger discs are slightly expanded. Strong digital scutes are present on all fingers.

The tibia length is 43–52 percent of SVL; the foot length is 41–49 percent of SVL. Relative lengths of appressed toes 4 > 3 > 5 > 2 > 1. The formula for the toe webbing (following Myers and Duellman, 1982) is **I** 1–2 **II** 1–2½ or 3 **III** 1 or 1½–3 **IV** 3–1 or 1½ **V**, with strong lateral fringes (weak on outer edges of toes 1 and 5) extending to the weakly expanded discs. A weak outer metatarsal fringe is present, as is a strong, curved tarsal keel that extends along the distal third of the tarsus and is continuous with the outer fringe on toe 1. Tuberculation consists of a large elliptical inner metatarsal tubercle, a round protuberant outer metatarsal tubercle, a single subarticular tubercle on toes 1 and 2, two on toes 3 and 5, and three on toe 4.

Adult males are smaller than adult females, presenting a SVL 73–95 percent of female SVL. Adult males generally have very large testes, roughly as large as the eye. The right testis is larger than the left and is situated more anteriorly in the body cavity.

It is likely that the size of the testis is a function of sexual activity, since in some adult specimens (= vocal slits open) the testes are not as enlarged as in others. The testes are unpigmented (= white) or are white with small black flecks; the black flecks are usually more concentrated near the lateral canals that connect with the kidneys. The maximum size of sexually immature males is evidenced by UVC 10133, a subadult male measuring 17.2 mm SVL with relatively small testes and only the left vocal slit open. The size at which females reach maturity is indicated by UVC 12261 and UVC 12568 which are subadult females that measure 20.6 mm and 20.7 mm SVL respectively, each with weakly differentiated ova and nonconvoluted oviducts. Mature oviducts are white or white with black flecks; both the immature ova of juvenile females and the enlarged differentiated ova of adults are white.

JAW AND THIGH MUSCULATURE: Both jaw and thigh musculature are identical to that usually found in dendrobatids. The posterodorsal portion of the tympanum is tilted beneath the superficial slip of the m. depressor mandibulae, which originates from the dorsal fascia; the deeper slips take their origins from the proximal portion of the otic ramus of the squamosal and the posterior edge of the tympanic ring. In light of the intraspecific variation in the presence of the m. adductor mandibulae externus superficialis (as opposed to the presence of only the m. adductor mandibulae posterior subexternus, the typical dendrobatid condition) in *Aromobates nocturnus* (Myers et al., 1991), we examined 10 specimens to determine the state of this character. All specimens exhibit only the m. adductor mandibulae posterior subexternus.

The thigh musculature does not differ significantly from that found in other dendrobatids. The distal tendon of the m. semitendinosus pierces that of the mm. gracilis complex before inserting on the knee. The m. gracilis minor is short, originating by its own tendon from the pelvic rim and extending less than a third the length of the thigh along the m. gracilis major before becoming indistinguishable from the latter. There is no indication that the m. semitendinosus tendon passes between these two muscles.

COLOR PATTERN: As is common in many species of *Colostethus*, the dorsal color pattern is variable. The dorsal ground color is tan, brown to blackish brown, or brown with a slight green tinge, or reddish yellow in some juveniles; in freshly preserved material the dorsal ground color consists of different shades of gray to black, while in older specimens it is light to dark brown. The dark dorsal pattern is dark brown to black in life (black in preservative) and varies from a definite X-shape to a multitude of indistinct blotches. Fingers 1–3 or 1–4 are white distally; the toes are generally darker with only the digital scutes white in some specimens. The limbs are dorsally brown or brown with an orange or yellow tinge. The thighs have either two or three blackish transverse bands dorsally. The cloacal tubercles are the same color as the thighs, black, or are light colored (cream to white). In most specimens there is a distinct white mark on either side of the cloaca on the dorsal surface of the thighs usually just above the cloacal tubercles; in some specimens the marks were reddish in life. The sides are the same color as the dorsum with small white spots and some white mottling below. The oblique postocular stripe is white and encompasses the entire visible tympanum (i.e., the anteroventral portion not hidden under the anterior edge of the superficial slip of the m. depressor mandibulae). A white flash mark is present at the dorsal base of the arm. Most juveniles present a very narrow incomplete cream or bronze dorsolateral stripe which seems to disappear ontogenetically in most cases; it consists of an anterior line extending posteriorly from the posterior corner of the eye to just past the arm insertion where it curves inward slightly, and a posterior line extending from near the cloaca along the dorsolateral ridge to almost half-way between the axilla and groin. In some adult specimens the anterior portion of the line can still be detected. A white spicule is present behind the angle of the jaws below and anterior to the oblique postocular stripe. A black stripe extends along the loreal region, through the nares, and around the tip of the snout; the area below this stripe is cream with occasional white spots and usually a black, roughly triangular spot situated below the anterior corner of the eye.

The ventral color pattern is sexually di-

Fig. 12. Extremes in ventral color pattern of *Colostethus atopoglossus*, new species, from left to right UVC 10125 and 10126, adult females collected the same day at the same locality. Approximately life size.

morphic in that males lack iridophores on the throat (fig. 10, right) while females are pure white. In both sexes the anterior belly (and throat in females) is white, often with black or gray spotting or mottling extending anteriorly to the lower lip (see fig. 12 for extremes in ventral pattern). The thighs, groin, and posterior belly are bright yellow-orange in life. The tibia are ventrally free of pigment. In preservative the yellow coloration fades and leaves the entire posterior venter white. There are at least two well defined, slightly raised white flecks arranged longitudinally along the ventral surface of the forearm, strong in life but hard to distinguish in some preserved specimens; in some specimens more than one fleck occurs distally, or the distal fleck may be located on the base of the hand. A black lower lip line extends from the angle of the jaws and fades near the anterior extreme. Palmar and plantar surfaces are brown.

### Distribution and Natural History

*Colostethus atopoglossus* is known only from the streams and along the road at the type locality, from 1800 to 2260 m in the Cordillera Occidental of Colombia. The site is referred to as El Boquerón, which is a somewhat indefinite place marking the border between the Departments Valle del Cauca and Chocó, 20 km from El Cairo, Department of Valle del Cauca.[14] In April 1996 the sign marking El Boquerón was bent and fallen over. The unfinished road that leads to El Boquerón departs from El Cairo and extends a distance of approximately 26 km. Traffic is restricted mainly to that of local inhabitants. Wood is constantly being extracted and pastures cleared, but to date there remains a huge expanse of undisturbed forest.

*Colostethus atopoglossus* is riparian. It is found mainly under rocks along small streams, although it can also be found in swampy grasses and in shallow, trickling streams with low vegetation. Several specimens were collected while they were actively hopping on rocks at the edge of the streams. Upon being disturbed, this species immediately dives into the water and buries itself in the substrate where it remains motionless for several minutes. Despite extensive nocturnal collecting, *C. atopoglossus* has not been found to be active after sundown, even on brightly lit nights when the moon is full.

Preliminary results of stomach content analysis of *C. atopoglossus* yield Arachnida, Hymenoptera, Orthoptera, Coleoptera (Bruchidae and Brentidae), and Diptera, and do not suggest any dietary specialization.

Males call from secluded positions beneath rocks or from vegetation in water. They have been observed to call with the upper body raised and the lower body in or out of the water, perched on leaves and twigs extending from the water. The call is a series of high-pitched notes given in $< 1$ sec (fig. 13).

The holotype was recorded for audiospectrographic analysis at the American Museum. The recording includes 18 calls in 4.8 min of tape. There are usually 13 notes in a range of 12–14 notes per call ($\bar{x} = 12.89$, $SD = 0.583$). Call duration is 0.797–0.959 sec ($\bar{x} = 0.8749$), depending mainly on the number of notes in a call. Each note is frequency modulated from lower to higher, as is evident in both narrow-band and wide-band spectrograms (fig. 13). The first several notes are given in ascending frequency, beginning at about 4160–4240 Hz for the start of the first note, which is much weaker than the others and which is the only one with most of its energy below 5 kHz; subsequent notes rise to an emphasized frequency of about 5800 Hz, with a slight decline in the terminal

[14] El Boquerón is defined as an *Inspección de Policía* by the Instituto Geográfico de Colombia "Agustín Codazzi" (1980: 210).

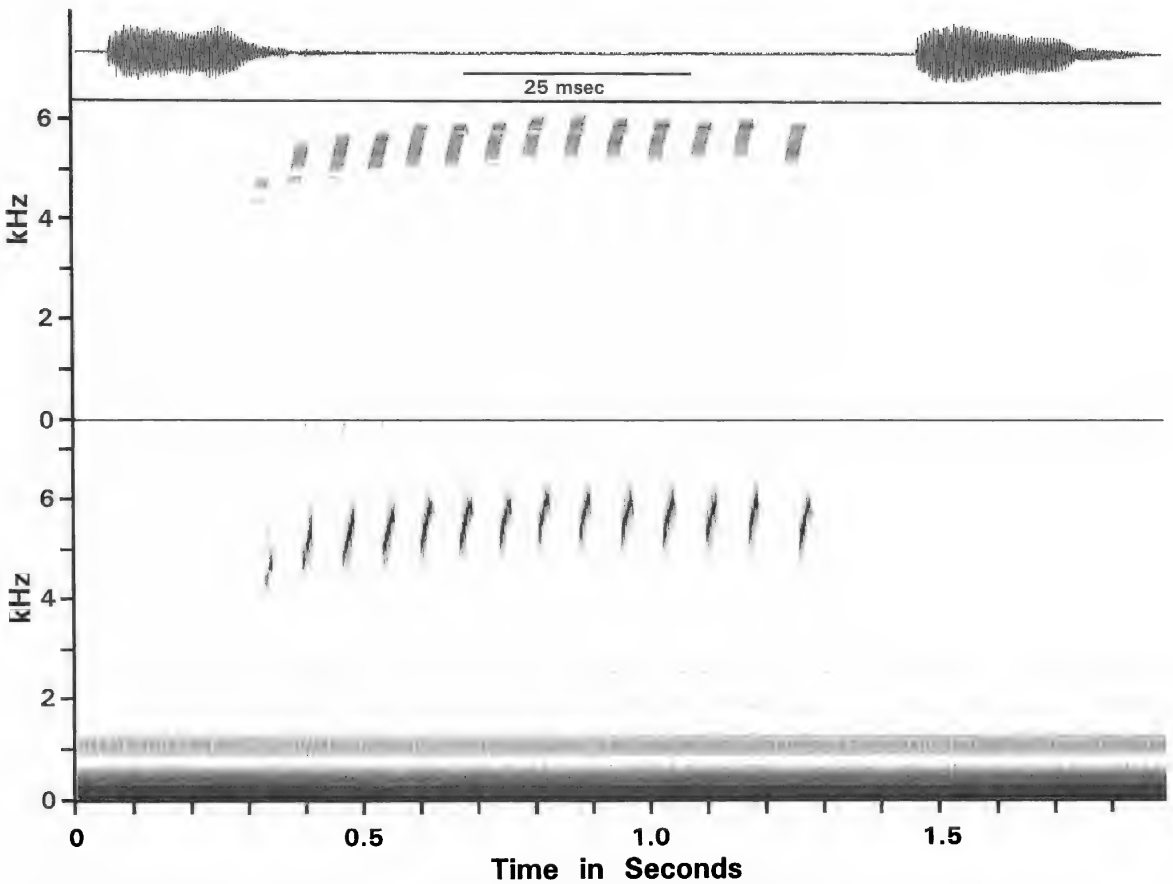


Fig. 13. A 14-note call from the holotype of *Colostethus atopoglossus*, new species. Uppermost sound spectrogram graphed with narrow-band 59-Hz filter, lowermost with wide-band 300-Hz filter. Waveforms are of last two notes in call. Recorded by T. Grant at type locality, April 4, 1996, 9:50 a.m., at air temperature of 18.8°C (spectrograms produced from tape copy on AMNH herpetology reel 276).

note(s). The notes are rapidly but weakly pulsed. Those shown in figure 13 are each ≤ 0.03 sec in duration.

Tadpoles of *Colostethus lehmanni* and at least one other *Colostethus*, presumably corresponding either to *C. atopoglossus* or *C. agilis* were collected in the streams where *C. atopoglossus* was found. Male nurse frogs of *C. lehmanni* were collected, enabling the identification of free swimming tadpoles; however, the tadpole of *C. agilis* is not identified in the literature and no tadpole carrying was observed in either of these species to permit positive larval identification.

Other anurans collected syntopically with *Colostethus atopoglossus* include *Atelopus chocoensis*, *Centrolene geckoideum*, *C. buckleyi*, *C. grandisonae*, *Cochranella griffithsi*, *Colostethus agilis*, *C. lehmanni*, *Eleutherodactylus babax*, *E. brevifrons*, *E. calcaratus*, *E. erythropleura*, *E. gracilis*, *E. restrepoi*, *E. silverstonei*, *E. thectopternus*, *E. w-nigrum*, *E. xylochobates*, and *Rhamphophryne* sp. Like *Colostethus atopoglossus*, *C. agilis* is diurnal and riparian and was collected on and under rocks along the same streams and road where *C. atopoglossus* was collected; no interaction between the two species has been observed.

## SYSTEMATICS

### Species Groups in *Colostethus*

Overall similarity and distribution suggest a sister-species relationship between the new *Colostethus atopoglossus* and *C. lacrimosus*,

both of which have a median lingual process. But no synapomorphies have been identified to support this speculation and we consider the lingual process to be a probable symplesiomorphy (see below). Because of unknown polarity and incomplete data on character distribution, several potentially indicative characters, such as the paired cloacal tubercles and a well-defined, white oblique postocular stripe, cannot be used to infer relationships with confidence. The postocular stripe is shared at least by *C. atopoglossus, C. lacrimosus,* and *C. parkerae*, with faint suggestion of such a marking also present in *C. chocoensis* (which lacks a lingual process).

At present, most species groups of *Colostethus* are defined by combinations of character states variously present in other groups, rather than by unambiguous synapomorphies, which have been hard to come by. Only two clades supported by unique synapomorphies have been identified, accommodating only six of the approximately 100 known species of *Colostethus* s.l.

Lynch (1982) described two species from the Cordillera Central of Colombia that are united by the apomorphic presence of a pronounced anal sheath (the *Colostethus edwardsi* group). To avoid "encumber[ing] future research with a needless name," Lynch (1982: 373) chose to relegate this group to *Colostethus* pending more extensive phylogenetic analysis. The character is not unique to dendrobatids as implied by Coloma (1995: 60), since the cloacal opening is concealed by an anal sheath or flap in diverse anurans.

Grant and Castro (MS) defined the *Colostethus ramosi* group by the derived presence of black glandular tissue on the ventral surface of the arm at the distal end of the humerus (= black arm band) in males for three named and one new species from the Andes of Colombia and Ecuador.

The *Colostethus inguinalis* group of Rivero ("1988" [1990]: 13) is a third group previously considered to be defined by synapomorphy, based on the swollen third finger of males. Myers et al. (1991: 18–19) did not cite this paper[15] but independently supported a geographically more extensive version of the group in suggesting that the same character could be used to define a restricted *Colostethus*. But the classification was not formalized and Myers (1991: 14) retreated from the position almost immediately because this character state is expressed in some *Epipedobates*. In reporting the character in a new *Colostethus* that also has the median lingual process, Myers and Donnelly (in press) now suggest that the "swollen third finger may prove to be yet another plesiomorphic trait that (like the various pale stripes) is variably expressed in dendrobatids and should be viewed cautiously until we know more about it."

Two species groups of *Colostethus* s.l. have been recently elevated to generic status, but there are problems of recognition even for these:

1. *Mannophryne* (La Marca, 1992) was erected for the *Colostethus collaris* group (= the *trinitatis* group of Rivero, "1988" [1990]: 18). The three character states[16] used to establish the monophyly of this group—dark throat collar, yellow throat, and elaborate aggressive and courtship behavior (fide La Marca, 1995: 54)—must be used in combination inasmuch as the throat collar is not confined to *Mannophryne* sensu La Marca (discussions in Myers et al., 1991: 19–23, fig. 15A, and Coloma, 1995: 59). Good behavioral information is available for only three of the eight named species treated by La Marca (literature summarized in Myers et al., 1991: 21–22, and La Marca, 1995: 46–50)—but, in general, the contrasting collar on a bright yellow throat appears to serve a visual function during female aggression. Therefore the "package" of color, color pattern, and associated behavior might characterize *Mannophryne* as a monophyletic albeit inadequately defined group of species that share a suite of morphological features that are relatively primitive within the Dendrobatidae.

2. An unresolved question of symplesiom-

[15] The 1988 issue of the journal containing Rivero's long-delayed paper was printed in February 1990 but not distributed until the following summer.

[16] A larval character (B1, large labial papillae) is shown as an additional synapomorphy in La Marca's cladogram (1995: 70). But his text (p. 53) shows that B1 applies only to *M. neblina* and that other species have the typical dendrobatid condition of small labial papillae.

orphy, homoplasy, or paraphyly is raised by the naming of *Nephelobates* (La Marca, 1994) for the *Colostethus alboguttatus* group, based on the presence of fanglike teeth, a character state also expressed in *Aromobates* (Myers et al., 1991: 27).

### *Colostethus* and the Ranoidea

The Dendrobatidae are now considered to be a well-defined family (even when the practical outgroup is all other frogs), but, within it, the speciose genus *Colostethus* s.l. seems to bristle with plesiomorphy. As suggested above, this has hindered phylogenetic analysis of the presumed basal groups of dendrobatids. Matters might be improved (one hopes) if the sister group of the family could be identified with confidence. But knowledge of dendrobatid relationships has been slow to increase—not surprising, perhaps, if we consider how long it took even to arrive at the *composition* of the family.

Cope (e.g., 1867: 189, 197) and Boulenger (1882) had trouble getting all the dendrobatids together, being confounded and misled by the presence or absence of teeth—characters then judged to be of major taxonomic importance, following their customary treatment as such in the *Erpétologie Général* of Duméril and Bibron (1841: 49–50). With the discovery of new taxa, Cope's division of Duméril and Bibron's toothless "Bufoniformes" faltered on the matter of teeth:

> It has been already pointed out [Cope, 1865] that the families of the toothless Anura, or Bufoniformia, are distinguishable into those with the arciferous and those with the raniform types of sternum. . . . and to the last [was assigned the] Dendrobatidae [= *Dendrobates* only]. Continued observation points to the radical nature of this diversity, while the increase of knowledge furnishes us with cases of rudimental dentition, indicating a less significance for the character which has been supposed to characterize the Bufoniformia. Such occurs in the genus *Colostethus* Cope, which seems to be quite identical with *Dendrobates*, except in the possession of teeth. (Cope, 1867: 189)

And later,

> The presence and absence of maxillary teeth is an important character . . . though the esteem in which I formerly held it has been much diminished by the discovery of . . . *Colostethus* Cope and *Eupemphix* Steindachner. (Cope, 1871: 200)

Nonetheless, Cope (1875: 7–8 ) retreated from this insight and came to consider the toothed dendrobatids (Colostethidae) as part of his Raniformia and the toothless ones (Dendrobatidae) as part of his Firmisternia—both groups being characterized by a "raniform sternal structure" versus an arciferous one, which "have about equal systematic value with the presence or absence of teeth."

Boulenger's (1882) *Catalogue of Batrachia Salientia* followed Cope's classification but somewhat simplified the scheme; the toothless and toothed dendrobatids were put under Firmisternia, in Ranidae and Dendrobatidae, respectively.

But Cope (1865: 112), followed by Boulenger (1882: 194), had *Phyllobates* s.l. far removed from other dendrobatids in a composite genus and composite family (Cystignathidae) of Arcifera. This, however, resulted from the lack of specimens. Later, having received information on the pectoral girdle of the holotype of *Phyllobates bicolor*, Boulenger (1888: 206) wrote, "I seize this opportunity to remark that the genus *Phyllobates*, Bibr., is a Ranoid, closely allied to and intermediate between *Hylixalus*, Espada, and *Prostherapis*, Cope."

Gadow (1901: 139, 237, 242, 272) mostly followed Boulenger's *Catalogue* but enlarged the Ranidae to encompass three subfamilies, including the Raninae (= Ranidae sensu Boulenger) and Dendrobatinae (= Dendrobatidae sensu Boulenger + *Cardioglossa*). Finally, Boulenger (1910: 152) dropped the family (or subfamily) Dendrobatidae and placed *Dendrobates* with four other related genera including *Colostethus* in one composite family, the Ranidae. Gadow and Boulenger recognized these genera as Neotropical ranids but not explicitly as a natural unit apart from all others.

Barbour and Noble (1920) submerged *Colostethus*[17] and other toothed dendrobatids

[17] *Colostethus* thereafter remained in synonymy until it was resurrected by Savage (1968: 747–748), who established the current concept of the genus. See Savage for a succinct historical summary of generic names that remain in synonymy and whose mention is unnecessary for present purposes.

into *Phyllobates*, in the Ranidae—but in the next several years Noble was to break away from classifications that allied dendrobatids with ranoids. Noble (1922: 8, 69) agreed with Boulenger's rejection of the family Dendrobatidae (mainly because it had come to contain the Old World *Mantella* and *Cardioglossa*) and placed *Dendrobates* and its toothed relatives, along with some other small frogs, in the Neotropical family Brachycephalidae.

Noble hypothesized a bufonid origin for the Brachycephalidae, which he regarded as a composite but natural[18] family, comprising three groups (Noble, 1926: 7):

> The second group of brachycephalid frogs may be clearly traced to their bufonid ancestors. This group includes only *Hyloxalus*, *Phyllobates*, and *Dendrobates*. . . . The immediate ancestor of this group is the bufonid *Crossodactylus* which possesses the same digital scutes. Its pectoral girdle shows an approach towards the firmisternal condition in the great reduction and slight overlap of the coracoid cartilages.

Finally, Noble (1931: 507) revived the subfamily name Dendrobatinae for the group and reaffirmed his belief that dendrobatids were derived from "the bufonid *Crossodactylus* or a form closely allied to it," or, more broadly (p. 504), from the bufonid Elosiinae (now leptodactylid Hylodinae). The Dendrobatinae were elevated back to family status by Davis in 1935.

Noble was the first investigator to have gathered all dendrobatids together as an explicitly monophyletic group, a view that has gone unchallenged for the last 70 years. Nearly 20 years after his death (in 1940 at age 47), Griffiths (1959) disputed Noble's ideas about broader relationships and argued that dendrobatids are ranoids after all, with similarities both to petropedetines and especially arthroleptids. Griffiths (1959: 483) proposed that "the Dendrobatinae be redefined as a neotropical subfamily of the Ranidae."

Griffiths marshalled to his proposal a suite of characters, one of which (the bursa angularis oris) was dismissed by Lynch (1971: 166) as being uninformative. Lynch (1971: 164–166) reargued Noble's elosiine (hylodine) hypothesis in light of Griffiths' character assessments. But it is hard to reach a balanced judgment from this literature because of mistaken observations in both camps. Lynch (1971: 164, 165), for example, erred in stating that some hylodines are toxic[19] and that the hylodine *Crossodactylus* shares with dendrobatids a ranoid pattern of attachment of the distal tendons of the thigh musculature.[20] Similarly, in arguing against Noble's interpretation of thigh muscles, Griffiths erroneously claimed to have demonstrated two patterns of thigh musculature in the Dendrobatidae, as follows:

1. A ranoid pattern in *Hyloxalus* [*Colostethus*] *bocagei*, in which the distal tendon of the m. semitendinosus inserts deeper (dorsad) than that of the m. gracilis (Griffiths, 1959: 470, fig. 13; also 1963: fig. 6i).
2. An "intermediate" pattern in *Phyllobates trinitatus* [= *Mannophryne trinitatis*], in which "the tendon of the semitendinosus lies dorsal to the massive gracilis major

[18] Noble was ambivalent as to whether higher taxa should necessarily be monophyletic, seemingly bending his views for geographic and pragmatic reasons. Although he suggested (1922: 9) that families should "embrace only natural assemblages," he also accepted polyphyletic groupings in some circumstances, as in 1926 (p. 7): "The brachycephalid frogs include at least three distinct groups of genera which seem to have arisen independently from bufonid ancestors. As all three, however, arose in the same general region and from the same family, I consider them a natural group. Such a procedure is in conformity with palæontological practice (Abel, 1909)." Noble (1931: 505) repeated this viewpoint when he assigned subfamilial names to the three groups. Davis (1935: 91) pointed out Noble's backsliding from "modern taxonomic conceptions" and elevated the groups to family status, but he botched matters in assigning an Indonesian toad to one of these families (see Inger, 1966: 74).

[19] To test this statement, Myers and Daly collected samples of eight species of *Crossodactylus*, *Hylodes*, and *Megaelosia* in Brazil in 1979. None were toxic, containing at most only very low levels of bufodienolide-like compounds. High levels of bufodienolides serve a defensive role in the Bufonidae but such compounds otherwise are suspected of being physiological regulators of $Na^+,K^+$-ATPase in amphibian skin (Flier et al., 1980; Daly et al., 1987: 1030, 1059).

[20] The common pattern in dendrobatids is neither ranoid nor bufonoid, but the pattern in *Crossodactylus* is bufonoid. The distal tendon of the m. semitendinosus inserts superficially (ventrad) to that of the m. gracilis complex in several specimens examined, including AMNH 103756 and 103760 (*Crossodactylus dispar*) and AMNH 103789 (*Crossodactylus* sp.). *Crossodactylus* therefore does not differ from other hylodines in this character.

but ventral to the much smaller gracilis minor" (Griffiths, 1959: 476, fig. 16; also 1963: fig. 6iii).[21]

In the first case (1) above, Silverstone (1975: 4) flatly disputed Griffiths' description for *Colostethus bocagei*. We concur with Silverstone based on dissection of the right thighs of AMNH 22170, 22171, and 89570; these specimens were verified as *C. bocagei* by Coloma (1995: 68), but Griffiths' identifications are taken on faith, since he gave no particulars on specimens received from various institutions (Griffiths, 1959: 484). *Colostethus bocagei* has the normal dendrobatid pattern in which the semitendinosus tendon enters the tendinous end of the gracilis complex (see below).

The common *Mannophryne trinitatis* also has the normal dendrobatid pattern (based on dissection of carcasses collected with AMNH 87392–87393), but, in the second case (2) above, Griffiths wrongly showed the tendon of the m. semitendinosus as passing between discrete tendons of insertion of the m. gracilis major and the m. gracilis minor. However, the gracilis major and gracilis minor have a common tendon or tendinous end that in most dendrobatids is entered or pierced by that of the m. semitendinosus (as in the illustrations of Noble, 1922: pl. 15, fig. 6, and Myers et al., 1991: fig. 6). Silverstone (1975: 4) found this last pattern in several dozen species of dendrobatids and we have seen only a few exceptions in an ongoing survey.[22] The piercing of the distal tendon or tendinous end of the m. gracilis complex by the distal tendon of the m. semitendinosus is generally considered a dendrobatid synapomorphy albeit not a unique one (see Noble, 1922: 40–41; Dunlap, 1960: 15).

Noble's (1922) dissections of thigh musculature appear to have been carefully done and elegantly presented, whereas Griffiths misinterpreted and inaccurately illustrated the two dendrobatids that he dissected. Griffiths' flawed descriptions of the thigh muscles do not support his thesis that dendrobatids should be placed as a subfamily of the Ranidae.

Also Griffiths (1959: 482) said that "Noble's claim that *Phyllobates* [*Colostethus subpunctatus*] has an arciferal stage cannot be upheld," and asserted that his own examination of specimens showed the contrary—but Griffiths did not mention Noble's (1926: 8, fig. 5) drawings of histological sections of the epicoracoid cartilages of *Phyllobates* [*Colostethus*] *subpunctatus*. Noble's clear histological evidence of overlap of the epicoracoids in *C. subpunctatus* was recently confirmed by Kaplan (1995), who curiously disclaimed any taxonomic relevance to the fact. Kaplan erroneously said that Noble had partly based his conclusions on an assumption that, "the overlap condition in *C. subpunctatus* is general for all dendrobatids," whereas Noble (1926: 10) explicitly stated that he found no such evidence in *Dendrobates*. According to Kaplan (1995: 302), inasmuch as the epicoracoid overlap "seems to be restricted . . . at the most to a small group of *Colostethus*, such a character should be considered irrelevant to the systematics of the whole family Dendrobatidae." But the condition is not "irrelevant" if it should prove homologous[23] with that in a sister group! Sufficient data are not at hand for a decision.

Ford (MS. and *in* Ford and Cannatella, 1993) simultaneously tested leptodactylid and ranoid hypotheses of dendrobatid relationships based on the same osteological characters. Ford concluded that the Dendrobatidae

[21] Based on the cited figures, the words dorsal and ventral are reversed in this quotation. Griffiths confused the sartorius and semitendinosus muscles in these drawings. In his 1959 paper, the m. sartorius is labeled "S," which (on p. 487) is keyed as "musculus semitendinosus," and the m. semitendinosus is labeled "ST," which is not to be found in the abbreviations list. The same sketches are republished in his following (1963) paper, but both the m. semitendinosus (fig. 6iii) and the m. sartorius (fig. 6i, ii, iii) are now labeled "ST" for semitendinosus. Although the sartorius and semitendinosus form a common muscle (sartorio-semitendinosus) in certain primitive frogs, they are separate in neobatrachians (Noble, 1922: 30–31; Dunlap, 1960).

[22] Unpublished data. Exceptions include specimens in the *Colostethus nubicola* complex (Grant and Myers, in preparation), some of which, curiously, *do* have a ranoidlike insertion of the m. semitendinosus! But polarity relative to the usual dendrobatid condition is not resolved and the taxa are not implicated in the literature being critiqued above.

[23] Kaplan's (1995: 302, 303) comments on homology are not persuasive, being mainly based on comparisons with *Acris*, *Bufo*, and *Spea*. Noble's thesis must be tested by comparison with hylodines, particularly *Crossodactylus*, whose "pectoral girdle shows an approach toward the firmisternal condition in the great reduction and slight overlap of the coracoid cartilages" (Noble, 1926: 9).

are a distinctive taxon embedded in the Ranoidea, thus supporting the main thrust of Griffiths' argument. Griffiths did not identify a most-closely related or sister group to dendrobatids as implied by figure 2 in Ford (1993). Aside from general characters, Griffiths (1959: 482–483) explicitly mentioned one similarity (supradigital scutes) to "petropedetid ranids" and several similarities (breeding, lack of vomerine teeth, sometimes a cartilaginous sternum) to "arthroleptid ranids." Ford's treatment (1993, fig. 3) showed the Arthroleptidae and part of a nonmonophyletic "Petropedetinae" as nearest outgroups to the Dendrobatidae. Ford's unpublished data matrix does not contain unambiguous synapomorphies uniting these groups, and, inasmuch as Griffiths' 1959 character analyses do not bear reexamination, the reader will search the literature in vain for *compelling* morphological evidence as to whether dendrobatids are most closely related to ranoids or to hylodines (see Ford, 1993, for pertinent literature).

Therefore, the median lingual process is of particular interest in providing new and independent evidence supporting dendrobatids as possible Neotropical ranoids. But this conflicts with recent evidence from mitochondrial DNA. Ruvinsky and Maxson's (1996: fig. 2) analysis shows the Dendrobatidae embedded within the Bufonoidea (= Hyloidea), as a sister group of all South American bufonoids (the sister taxon of all Neotropical taxa being the Telmatobiinae [assuming the monophyly of this group and using the Cuban *Eleutherodactylus cuneatus* as the sole exemplar]). However, molecular evidence is not yet in for any of the three genera of Hylodinae (Elosinae) or for any of the 16 ranoid genera (in six subfamilies) that possess a median lingual process.[24] At the present stage of knowledge, data from at least the Hylodinae and Petropedetinae are needed in order to place these groups and Dendrobatidae more convincingly within a neobatrachian phylogeny. Evidence provided by the median lingual process also must be followed up in greater detail than we can provide in the present paper, and consideration should be given to other aspects of tongue morphology for which only fragmentary data are available (e.g., mucosal epithelium with filiform papillae vs. ridgelike folding; presence or absence of a ciliated collar around the taste disc—see Surface Ultrastructure and Other Lingual Characters).

The widespread occurrence of the median lingual process in certain African and Asian ranoids, and the apparent absence of such a structure in all other frogs except certain *Colostethus*, suggests a ranoid relationship for dendrobatids if this character is considered in isolation. Even so, occurrence of either homoplasy or independent loss of the lingual process in several ranoid lineages complicates matters, and the confused state of ranoid systematics prevents immediate determination as to where the lingual process or processes should be considered synapomorphic. At this time, homology of the distinctive types of lingual process seems suggested only by the widespread existence of a retractile mechanism in the Old World ranoids and the apparent loss of this (or a similar) mechanism in some, but not all, petropedetines.

In addition to being nonretractile, the dendrobatid lingual process shows greatest structural resemblance to that in certain petropedetines. So, pending further investigation, we consider the lingual process as being probably homologous at least in dendrobatids and the Petropedetinae. Africa must therefore be kept in mind as a source of suitable outgroups when contemplating phylogenetic analysis of the basal portion of the dendrobatid clade.

Myers et al. (1991) hypothesized *Aromobates* as the plesiomorphic sister group of all other dendrobatids. The variable presence in specimens of *Aromobates nocturnus* of a muscle (m. adductor externus superficialis) lacking in other dendrobatids is consistent with the dendrobatid-ranoid hypothesis but not the dendrobatid-leptodactylid hypothesis (Myers et al., 1991: 26; Ford, 1993: 225–226). The absence of a median lingual process in *Aromobates* does nothing to elucidate relationships if this structure is indeed an ancient ranoid plesiomorphy that has only a relic occurrence in a few *Colostethus*.

In addition to the primitive jaw musculature, *Aromobates* stands apart from all other dendrobatids in using a volatile mercaptanlike

[24] There was a report aligning *Rhacophorus* with Hylidae (Hedges and Maxson, 1993), but this was an error as explained by Hay et al. (1995: 933), who informally reported that a partial sequence from *Rhacophorus pardalis* grouped it with ranoids as expected.

compound for chemical defense—a presumed autapomorphy (but see Myers et al., 1991: 28). It is additionally unique among dendrobatids in being nocturnal,[25] in being aquatic (vs. riparian, terrestrial, or arboreal), and in being larger; these traits were hypothesized as being primitive for the family but with recognition that they too might be autapomorphic. In any case, *Aromobates* is symplesiomorphic in osteological features with members of the former *Colostethus collaris* group (= *Mannophryne*, see above), which also may be near the base of the dendrobatid clade.

We have yet to examine the osteology of any of the named or unnamed species of *Colostethus* that have a median lingual process, for which reason we decline further speculation at this time. But these species already seem to have performed an important role in providing new and entirely unexpected evidence that dendrobatids may be New World ranoids, as originally indicated by Cope and claimed by Boulenger in the late 19th and early 20th centuries. However, all hypotheses of dendrobatid relationships remain vague and little is gained by claiming certainty for one view or another.[26]

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[25] This is not to be confused with the crepuscular tendencies of some dendrobatids or, in the case of occasional *Colostethus*, with exceptionally long diel cycles of activity that sometimes extend from day into night. Coloma (1995: 58) mentioned captive specimens of several *Colostethus* spp. as being "facultatively nocturnal," but the phenomenon also occurs under natural conditions (Myers et al., 1991: 27–28).

[26] Having said that, we take perverse pleasure in advertising the recent discovery of an additional apomorphy shared by the Dendrobatidae and two of the three genera of South American Hylodinae (Burton, MS.). It needs remembering that Noble's hypothesis of a dendrobatid-hylodine relationship has *not* been truly discredited and that the affinities of the hylodines (elosiines) are still unclear (Lynch, 1971: 207). As indicated herein, Noble's anatomical observations have been corroborated whereas those of his main critic (Griffiths) have not.

## APPENDIX 1: SPECIMENS OF *COLOSTETHUS* (DENDROBATIDAE) SHOWING A MEDIAN LINGUAL PROCESS

Collection sources and abbreviations are: American Museum of Natural History amphibian collection (**AMNH**), Museo de la Estación Biológica de Rancho Grande (**EBRG**), Instituto de Ciencias Naturales, Universidad Nacional (**ICN**), University of Kansas Natural History Museum (**KU**), Natural History Museum of Los Angeles County (**LACM**), Museo de Biología de la Universidad Central de Venezuela (**MBUCV**), Museum of Comparative Zoology (**MCZ**), National Museum of Natural History, Smithsonian Institution (**USNM**), Universidad del Valle (**UVC**).

*Colostethus atopoglossus* Grant, Humphrey, and Myers, Colombia (58 specimens in UVC type series, this paper)

*Colostethus lacrimosus* Myers, Colombia (AMNH 88828–88830, 110747–110753, 110789; KU 170243, 170244; ICN 13425, 13426; LACM 55815; UVC 7293–7296, 6257, 6267, 8802)

*C. parkerae* Meinhardt and Parmelee, Venezuela (KU 167328–167333)

*C. shrevei* Rivero, Venezuela (AMNH 23196, 23197; MCZ 27833, 28567)

*Colostethus* species (*C. chocoensis* auct.), Ecuador (AMNH 104819–104824; KU 166157, 166158, 221616)

*Colostethus* species, Venezuela (Myers and Donnelly, in press, AMNH 131341–131342, 131345, 131347; MBUCV 6430–6433)

*Colostethus* species, Venezuela (AMNH 118691)

*Colostethus* species, Venezuela (AMNH and EBRG uncataloged [field nos. CWM 19143–19155, 19307, 19308, 19336–19353])

## APPENDIX 2: SPECIMENS OF OLD WORLD RANOID FROGS DOCUMENTED FOR PRESENCE OF MEDIAN LINGUAL PROCESS

The following arrangement follows Frost (1985) except for a few recent changes at the species level. Catalog numbers in parentheses are those of the amphibian collection, American Museum of Natural History (AMNH). The specimens cited were explicitly noted as having a median lingual process. Four genera are included based on species not seen but documented by authoritative literature citation; other such genera are likely to have been overlooked.

Many of the species determinations originally were made or subsequently verified by authorities in African and Asian herpetology (e.g., Laurent, Loveridge, Noble, Poynton, Witte, Zweifel). Nonetheless, misidentifications are certain to occur. A record of specimens examined is essential for this reason and also because of the likelihood that understanding of species limits will change with time, leading to necessary changes in the use of many names.

ARTHROLEPTIDAE: ARTHROLEPTINAE

*Arthroleptis adolfifriderici* (68668, 72748, 72752, 72759–72762)

*Arthroleptis francei* (136606)

*Arthroleptis poecilonotus* (3140, 6746–6749, 6694, 8971–8974, 140806–140808)

*Arthroleptis stenodactylus* (12635–12641, 56104, 56105)

*Arthroleptis tanneri* (68669)

*Arthroleptis variabilis* (8986–8992, 8995–9000, 9002–9011, 9013, 9014, 9016–9022, 9024–9031, 9033, 9035, 9036)

RANIDAE: PETROPEDETINAE

*Arthroleptides dutoiti* (68670–68677)

*Arthroleptides martiensseni* (37281, 37282)

*Dimorphognathus africanus* (11890)

*Ericabatrachus baleensis* (fide Largen, 1991)

*Nothophryne broadleyi* (95098, 95099)

*Petropedetes cameronensis* (23612)

*Petropedetes johnstoni* (24015)

*Petropedetes newtoni* (3138, 6687, 14369)

*Petropedetes palmipes* (23936)

*Phrynobatrachus accraensis* (83331, 83333, 83335, 83337, 83345, 83349, 145889)

*Phrynobatrachus acridoides* (56074, 56077, 68731–68755, 87532–87551)

*Phrynobatrachus acutirostris* (23568)

*Phrynobatrachus alleni* (84642, 84643)

*Phrynobatrachus aelleni* (145893, 145896)

*Phrynobatrachus alticola* (84644)

*Phrynobatrachus batesii* (11887–11889)

*Phrynobatrachus bequaerti* (79898, 79899)

*Phrynobatrachus cricogaster* (63521, 63522)

*Phrynobatrachus cryptotis* (79900, 79901)

*Phrynobatrachus dendrobates* (9114, 9116, 9117, 9119–9121, 9124, 9126, 9129–9132, 9134, 68739)

*Phrynobatrachus feae* (8979, 8980)

*Phrynobatrachus fraterculus* (145898, 145899)

*Phrynobatrachus graueri* (68773, 68778, 68884, 68917, 72888–72893, 733304, 79902, 79903)

*Phrynobatrachus gutturosus* (79904, 79905, 83330, 83340–83342, 83347, 83348, 84645)

*Phrynobatrachus kinangopensis* (87601–87613)

*Phrynobatrachus krefftii* (68742, 116658)

*Phrynobatrachus mababiensis* (129781–129804)

*Phrynobatrachus minutus* (12621, 12624, 12631, 12632, 79906, 79907)

*Phrynobatrachus natalensis* (3192, 3193, 5213–5216, 23335, 37563, 37575, 73931, 73932, 83321, 83322, 83350, 83390, 83392, 83393)

*Phrynobatrachus parkeri* (79908, 79909)

*Phrynobatrachus parvulus* (8978, 68774–68776, 79910)
*Phrynobatrachus perpalmatus* (9138, 9140–9143, 9145–9147, 9156–9158, 9160–9164)
*Phrynobatrachus petropedetoides* (129563, 129564, 129574, 129586)
*Phrynobatrachus plicatus* (3141, 6692, 6771, 72901, 72913)
*Phrynobatrachus rouxi* (68762–68764)
*Phrynobatrachus scapularis* (9039–9042, 9045)
*Phrynobatrachus ukingensis* (33876)
*Phrynobatrachus versicolor* (23567, 68749–68752, 87461–87465)
*Phrynodon sandersoni* (fide Parker, 1935)

RANIDAE: MANTELLINAE
*Mantidactylus femoralis* (23780, 23781, 50361, 50362, 50365–50368, 50520–50522)

RANIDAE: RANINAE
*Discodeles bufoniformis* (67654, 71842)
*Discodeles guppyi* (64274–64279)
*Discodeles opisthodon* (35436)
*Indirana leithii* (40034, 63509)
*Micrixalus*, various spp. (Boulenger, 1882; Satyamurti, 1967: 35; Dubois, "1986" [1987]: 54)
*Platymantis boulengeri* (64627, 64254, 70074)
*Platymantis gilliardi* (23545–23547)
*Platymantis dorsalis* (52753, 88045)
*Staurois natator* (70013)

RHACOPHORIDAE: PHILAUTINAE
*Philautus eximius* (fide Shreve, 1940, and Dutta and Manamendra-Arachchi, 1996: 162, 168).

RHACOPHORIDAE: RHACOPHORINAE
*Rhacophorus macropus* (74210, 74211)

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